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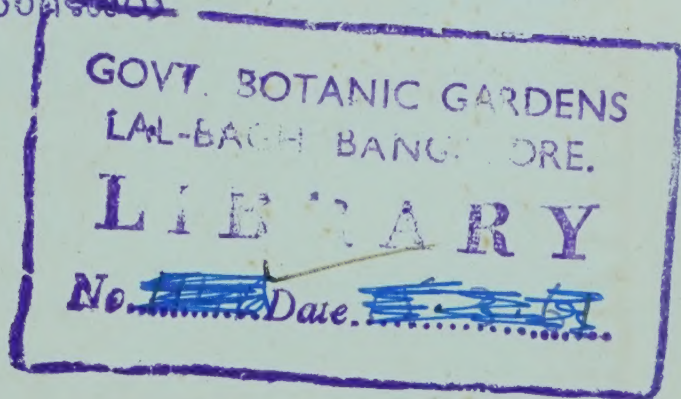
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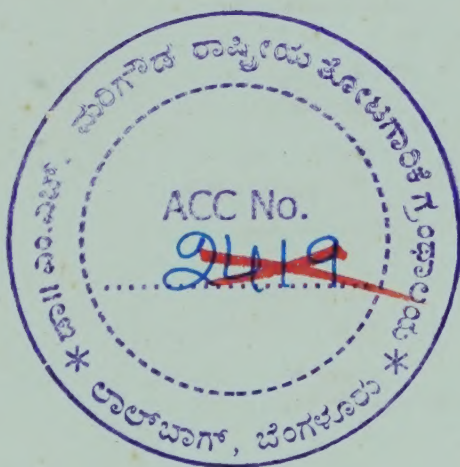
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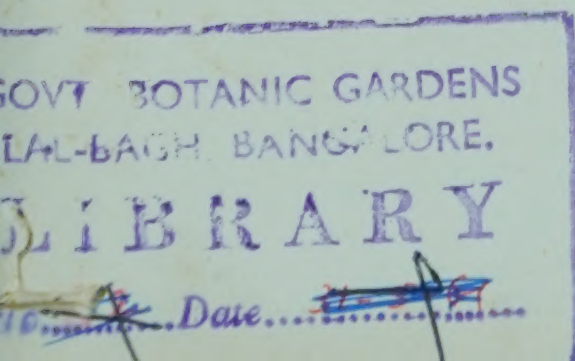
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Introduction to
ENTOMOLOGY

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Protective resemblance of the Indian butterfly, *Kallima inachus*, to a withered or diseased leaf



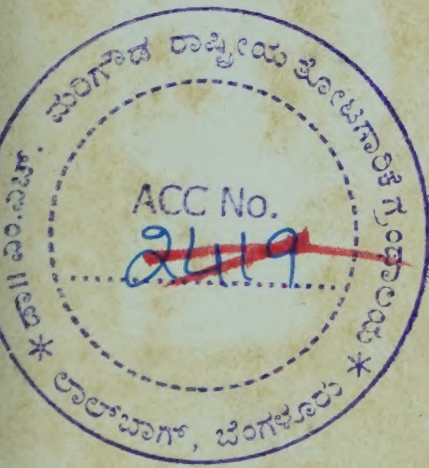
Introduction to ENTOMOLOGY

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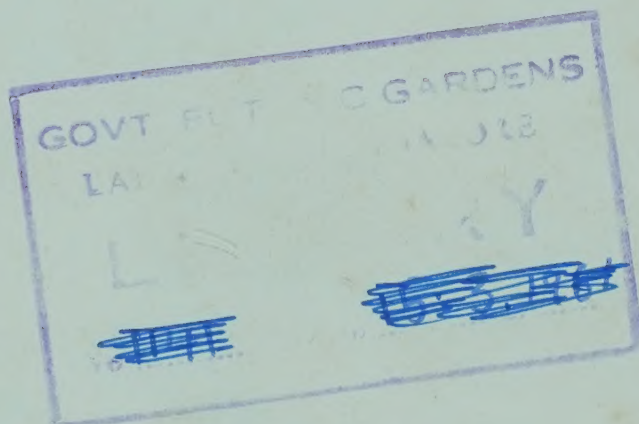
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Contents

PART ONE

GENERAL ANATOMY AND CLASSIFICATION

1. The Insects

Systematic position	19
Origin of the insects	23

2. External Morphology

General structure	27
The integument	27
Sclerites and membranes—pigmentation—microsculpture— cuticular processes—stridulating organs	
The head	31
The cranium—the eyes—the antennae—the mouthparts	
The thorax	42
The thoracic segments—tergites—sternites—pleurites	
The legs	44
Coxa—trochanter—femur—medius and tibia—tarsus— empodium—specialization of the legs	
The wings	49
Modifications of the wings—structure of the wing—wing venation	
The abdomen	53
Number of segments—position of the anus and genital orifice—abdominal appendages—male copulatory apparatus	

3. Internal Anatomy

The digestive system	57
Fore, middle and hind gut	
The respiratory system	59
Spiracles—tracheae—gills of insects—respiration	
The circulatory system	62
Haemocoele—dorsal vessel	
The excretory organs	63
Malpighian tubules—pericardial cells—oenocytes—fat body—luminous organs	

The nervous system	65
Central nervous system—brain—visceral nerve system— peripheral nerve system—corpora allata	
The sense organs	67
Organs of touch—smell and taste—sight—chordotonal organs	
The reproductive organs	71
Female organs—male organs	
4. Development	
Embryonic development	74
Formation of the embryo—the stages of embryonic development	
Postembryonic development	76
Hatching—metamorphosis—the larva—the pupa—the adult (imago)—hypermetamorphosis	
Developmental anomalies	82
Parthenogenesis — polyembryony — viviparity — paedo- genesis—prothetely—foetometamorphosis	
5. A General Classification of the Insects	
The major divisions	85
The evolution of wings	85
Sub-Class <i>COLLEMBOLA</i> :	87
1. Order <i>Collembola</i>	
Sub-Class <i>PROTURA</i> :	87
2. Order <i>Protura</i>	
Sub-Class <i>THYSANURA</i> :	90
3. Order <i>Entotropha</i>	
4. Order <i>Ectotropha</i>	
Sub-Class <i>PTERYGOTA</i> :	90
A. Section Palaeoptera	90
Superorder PALAEODICTYOPTERA	91
5. Order <i>Eupalaeodictyoptera</i>	
6. Order <i>Protohemiptera</i>	
7. Order <i>Megasecoptera</i>	
Superorder EPHEMEROPTERA	91
8. Order <i>Protephemeroptera</i>	
9. Order <i>Plecoptera</i>	
Superorder ODONATOPTERA	98
10. Order <i>Meganisoptera</i>	
11. Order <i>Odonata</i>	

B. Section Polyneoptera	98
Superorder BLATTOPTEROIDEA	98
12. Order <i>Dictyoptera</i>	
13. Order <i>Protoblattoptera</i>	
14. Order <i>Isoptera</i>	
15. Order <i>Zoraptera</i>	
Superorder ORTHOPTEROIDEA	99
16. Order <i>Protorthoptera</i>	
17. Order <i>Plecoptera</i>	
18. Order <i>Notoptera</i>	
19. Order <i>Phasmoptera</i>	
20. Order <i>Orthoptera</i>	
21. Order <i>Embioptera</i>	
Superorder DERMAPTEROIDEA	101
22. Order <i>Protelytroptera</i>	
23. Order <i>Dermaptera</i>	
C. Section Oligoneoptera	101
Superorder COLEOPTEROIDEA	101
24. Order <i>Coleoptera</i>	
Superorder NEUROPTEROIDEA	102
25. Order <i>Megaloptera</i>	
26. Order <i>Raphidioptera</i>	
27. Order <i>Planipennia</i>	
Superorder MECOPTEROIDEA	103
28. Order <i>Mecoptera</i>	
29. Order <i>Trichoptera</i>	
30. Order <i>Lepidoptera</i>	
31. Order <i>Diptera</i>	
Superorder SIPHONAPTEROIDEA	106
32. Order <i>Siphonaptera</i>	
Superorder HYMENOPTEROIDEA	106
33. Order <i>Hymenoptera</i>	
34. Order <i>Strepsiptera</i>	
D. Section Paraneoptera	107
Superorder PSOCOPTEROIDEA	107
35. Order <i>Psocoptera</i>	
36. Order <i>Mallophaga</i>	
37. Order <i>Anoplura</i>	
Superorder THYSANOPTEROIDEA	108
38. Order <i>Thysanoptera</i>	

PART TWO

BIOLOGY

6. Physiology

Nutrition	113
Feeding habits—digestion—extra-oral digestion—intestinal digestion—mycetomes—metabolism	
Excretion	121
Malpighian tubules—fat body—luminous organs—miscellaneous secretions	
Respiration	124
Transport of oxygen by the tracheae—aquatic insects—cutaneous respiration—blood-gills—tracheal gills—tracheal respiration—capture of oxygen from plants	
Circulatory system	130
The blood	
Sense organs	131
Sight—smell—taste—hearing—other senses	
Tropisms	137
Phototropism—thermotropism—hygrotropism—chemotropism—thigmotropism	
Reproduction	147
Sex-determination — parthenogenesis — sexual characteristics—mating—egg-laying—care of eggs and larvae	

7. Behaviour

Simple behaviour-patterns	159
Walking—jumping—digging—swimming—flying	
Means of attack	162
Active pursuit—traps	
Defensive mechanisms	164
Piercing organs—defensive secretions—reflex bleeding—shields, and attitudes of defence—reflex immobility—shedding and regeneration of limbs—natural and artificial shelter and camouflage	
Mimicry and protective colouration	171
Cryptic colouration and shape—mechanism and purpose of cryptic colouration—warning colours—mimicry—different categories of mimicry—an explanation of mimicry	

Parasitism	181
Commensals—symbionts—inquilines—endoparasites—ecto-parasitism and phoresy	
Conscious behaviour	183
Conditioned reflexes—drill—labyrinths—taking bearings, and finding the way back to the nest—language—use of tools	
8. Social Life	
The solitary instinct	191
Aspects of social life	192
Crowds—social groups—static groups—active groups—biocenosis, or societies	
The social insects	200
Wasps—bumble-bees— <i>Meliponinae</i> —hive-bees	
The ants	204
Driver-ants—harvesting-ants—mushroom gardens—honey ants—ant-stables—slave-making ants—myrmecophiles, or commensals of ants	
The termites	212
Castes—foundation of a colony—nutrition—types of termitarium—PROTERMITIDAE—MESOTERMITIDAE—METATERMITIDAE—termitophilous insects—enemies of termites	

PART THREE

PALAEONTOLOGY AND GEOGRAPHICAL DISTRIBUTION

9. The Evolution of Insects	229
The antiquity of the insects	230
The major land-masses, or 'asylums'	232
The major groups of Pterygote insects	239
10. The Fossil Insects	
Sub-Class <i>COLLEMBOLA</i>	240
1. Order <i>Collembola</i>	
Sub-Class <i>PROTURA</i>	241
2. Order <i>Protura</i>	
Sub-Class <i>THYSANURA</i>	241
3. Order <i>Entotropha</i>	
4. Order <i>Ectotropha</i>	

Sub-Class <i>PTERYGOTA</i>	241
Section Palaeoptera	241
5. Order <i>Eupalaeodictyoptera</i>	
6. Order <i>Protohemiptera</i>	
7. Order <i>Megasecoptera</i>	
8. Order <i>Protephemeroptera</i>	
9. Order <i>Plectoptera</i>	
10. Order <i>Meganisoptera</i>	
11. Order <i>Odonata</i>	
Section Polyneoptera	265
12. Order <i>Dictyoptera</i>	
13. Order <i>Protoblattoptera</i>	
14. Order <i>Isoptera</i>	
15. Order <i>Zoraptera</i>	
16. Order <i>Protorthoptera</i>	
17. Order <i>Plecoptera</i>	
18. Order <i>Notoptera</i>	
19. Order <i>Phasmoptera</i>	
20. Order <i>Orthoptera</i>	
21. Order <i>Embioptera</i>	
22. Order <i>Protelytroptera</i>	
23. Order <i>Dermaptera</i>	
Section Oligoneoptera	288
24. Order <i>Coleoptera</i>	
25. Order <i>Megaloptera</i>	
26. Order <i>Raphidioptera</i>	
27. Order <i>Planipennia</i>	
28. Order <i>Mecoptera</i>	
29. Order <i>Trichoptera</i>	
30. Order <i>Lepidoptera</i>	
31. Order <i>Diptera</i>	
32. Order <i>Aphaniptera</i>	
33. Order <i>Hymenoptera</i>	
34. Order <i>Strepsiptera</i>	
Section Paraneoptera	304
35. Order <i>Psocoptera</i>	
36. Order <i>Mallophaga</i>	
37. Order <i>Anoplura</i>	
38. Order <i>Thysanoptera</i>	
39. Order <i>Homoptera</i>	
40. Order <i>Heteroptera</i>	

11. How the Insects Spread Over the Earth	311
The First Pterygote Insects	311
The Succession of Faunas among the Insects	312
A. <i>The Laurentian fauna of the Palaeozoic</i>	313
The Carboniferous fauna—the Permian fauna	
B. <i>The primitive Gondwanian forms</i>	315
C. <i>Gondwanaland in the Mesozoic</i>	316
The Palaeantarctic groups—Inabresia—the Africano-Brazilian lines—the Eastern Gondwanian stocks	
D. <i>The Tertiary fauna of Angara Land</i>	320
The Angarian stocks—the colonization of Europe—the colonization of the Mediterranean—the colonization of the Holarctic Region—the colonization of North America	
The Natural Regions of the World	327
Australian Region — Neotropical Region — Ethiopian Region—Oriental Region—Holarctic Region	

Plates

Protective resemblance of the Indian butterfly, <i>Kallima inachus</i> , to a withered or diseased leaf	Frontispiece
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PART ONE

	Page
I Classes of Arthropods other than insects	21
II Mouthparts of insects	41
III Some examples of larvae	79
IV Primitive wingless insects (<i>APTERYGOTA</i>)	89
<i>Collembola</i>	
<i>Protura</i>	
<i>Thysanura</i>	
V Pterygote insects (<i>POLYNEOPTERA</i>)	93
<i>Isoptera</i>	
<i>Zoraptera</i>	
<i>Notoptera</i>	
<i>Embioptera</i>	
<i>Dermaptera</i>	
VI Pterygote insects (<i>OLIGONEOPTERA</i> and <i>PARANEOPTERA</i>)	95
<i>Siphonaptera</i>	
<i>Strepsiptera</i>	
<i>Psocoptera</i>	
<i>Mallophaga</i>	
<i>Anoplura</i>	
<i>Thysanoptera</i>	
<i>Homoptera</i>	
<i>Heteroptera</i>	
VII (<i>Colour</i>) Pterygote insects (<i>PALAEOPTERA</i> and <i>POLYNEOPTERA</i>)	facing 96
<i>Plectoptera</i>	
<i>Odonata</i>	
<i>Plecoptera</i>	

VIII	(Colour) Pterygote insects (POLYNEOPTERA)	<i>facing</i> 97
	<i>Dictyoptera</i>	
	<i>Cheleutoptera</i>	
	<i>Orthoptera</i>	
IX	(Colour) Pterygote insects (OLIGONEOPTERA)	<i>facing</i> 104
	<i>Coleoptera</i>	
	<i>Megaloptera</i>	
	<i>Raphidioptera</i>	
	<i>Planipennia</i>	
X	(Colour) Pterygote insects (OLIGONEOPTERA)	<i>facing</i> 105
	<i>Mecoptera</i>	
	<i>Trichoptera</i>	
	<i>Lepidoptera</i>	
	<i>Diptera</i>	
	<i>Hymenoptera</i>	
XI	(Colour) <i>Ascalaphus libelluloides</i>	<i>facing</i> 108
XII	(Colour) <i>Cupes raffrayi</i>	<i>facing</i> 109

PART TWO

I	The copulation of insects	149
II	The oviposition of insects	153
III	(Colour) Cryptic colouration—leaves	<i>facing</i> 144
IV	(Colour) Cryptic colouration—twigs and bark	<i>facing</i> 145
V	(Colour) Cryptic colouration—bark and stones	<i>facing</i> 152
VI	(Colour) Mimicry in insects	<i>facing</i> 153
VII	Care of the young	154
VIII	Ants	209
IX	Nests of ants and termites	217
X	Termites	223

PART THREE

I	A Carboniferous forest	235
II	Fossil insects (PALAEODICTYOPTERA)	245
III	Fossil insects (PALAEODICTYOPTERA)	249

IV	Fossil insects:	253
	<i>Protohemiptera</i>	
	<i>Megasecoptera</i>	
	<i>Meganisoptera</i>	
V	Fossil insects:	260
	<i>Meganisoptera</i>	
VI	Fossil insects:	263
	<i>Protephemeroptera</i>	
	<i>Plectoptera</i>	
	<i>Odonata</i>	
VII	Fossil insects:	269
	<i>Dictyoptera</i>	
VIII	Fossil insects:	273
	<i>Protoblattoptera</i>	
IX	Fossil insects:	277
	<i>Protorthoptera</i>	
X	Fossil insects:	283
	<i>Plecoptera</i>	
	<i>Phasmoptera</i>	
	<i>Orthoptera</i>	
XI	Fossil insects:	293
	<i>Protelytroptera</i>	
	<i>Dermaptera</i>	
	<i>Coleoptera</i>	
	<i>Raphidioptera</i>	
	<i>Planipennia</i>	
XII	Fossil insects:	303
	<i>Lepidoptera</i>	
	<i>Diptera</i>	
	<i>Aphaniptera</i>	
	<i>Hymenoptera</i>	
	<i>Strepsiptera</i>	
XIII	Fossil insects:	307
	<i>Psocoptera</i>	
	<i>Homoptera</i>	
	<i>Heteroptera</i>	
XIV	Map of the natural regions of the world	330

PART ONE

GENERAL ANATOMY AND CLASSIFICATION

1

The Insects

INSECTS belong to the great phylum Arthropoda (or Articulated Animals), because they have the body made up of a series of segments (or somites). The segments of the body are of different kinds, and are arranged into three groups: the head, the thorax and the abdomen. The number of segments remains fixed after the early stages of embryonic development, and this number does not increase during the life of the insect, except in the Protura. We can recognize six segments in the head, three in the thorax, and twelve in the abdomen, in all groups except the Collembola, which have only six abdominal segments.

Only a single pair of antennae exists, and even these are absent in the Protura. There are three pairs of thoracic legs. Respiration is by means of tracheae, opening to the exterior through pairs of spiracles (stigmata). The genital ducts open on the posterior part of the abdomen. Post-embryonic development is rarely continuous, and there are nearly always metamorphoses. When the insect has a complete metamorphosis, it passes through three postembryonic stages, after emerging from the egg: larva, pupa and imago (or adult).

Insects are by far the most numerous Class of the Animal Kingdom. Round about one million species have been described, and an average of 6,000 to 7,000 are added each year. Moreover, the most reliable estimates of the total number of insects, known and unknown, that exist in the world rise as high as four to five millions.

SYSTEMATIC POSITION

Since the Insecta form a Class within the Phylum Arthropoda, it is helpful to start by recalling the general characteristics of the latter.

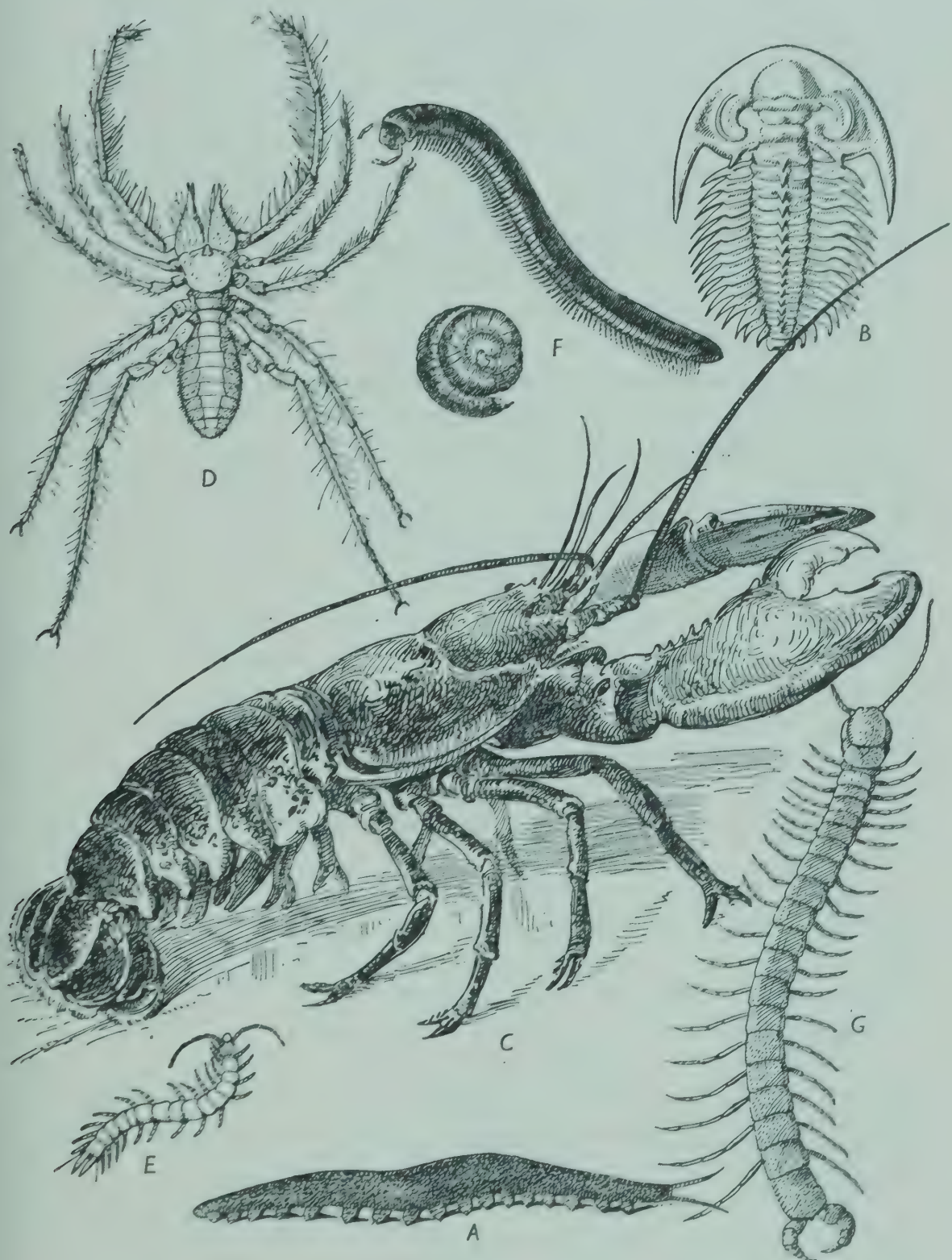
The body of an Arthropod is segmented, protected by an external skeleton which is formed from rigid plates (sclerites) articulated together. Primitively, each segment of the body (or somite) bears one pair of jointed appendages (hence the name Arthropoda), but on certain segments these appendages have become specialized for one particular function: some as mouthparts, others as limbs for walking or for grasping, others as genital organs.

The internal organization of the Arthropoda shows certain important characteristics. The blood is not enclosed in a complete circulatory

PLATE 1 – I. ARTHROPODS OTHER THAN INSECTS

- A. Class **Onychophora**. *Peripatus capensis* (after SEDGWICK).
- B. Class **Trilobita**. *Holmia kjerulfi*, a Lower Cambrian fossil (after HOLM).
- C. Class **Crustacea**. *Homarus vulgaris*, Decapoda.
- D. Class **Arachnida** (Chelicerata). *Galeodes araneoides*, Solifuga, from southern Russia (after BLANCHARD).
- E. Class **Progoneata**. *Scolopendrella immaculata*, Symphyla, from France (after BERLESE).
- F. Class **Progoneata**. *Pachyiulus varius*, Diplopoda, one specimen on the move, and another rolled up (after BERLESE).
- G. Class **Opisthogoneata**. *Scolopendra cingulata*, Chilopoda (after BERLESE).

PLATE 1-I. ARTHROPODS OTHER THAN INSECTS



system, but is distributed through the general cavity of the body (haemocoel) by a heart which is supplied with lateral openings (ostioles), and which lies dorsally to the alimentary canal. The nervous system consists of a peri-oesophageal collar, with a dorsal brain, and a ventral chain of ganglia. With rare exceptions all the muscle is striated. There is no ciliated epithelium.

Formerly, the **Onychophora** (Pl. 1. I (A), *Peripatus*) were included in the Arthropoda. These are strange animals which look like caterpillars, and are carnivorous, living in rotten wood in tropical countries, and pursuing their prey, which they trap with jets of sticky saliva. *Peripatus* is a survivor of a very ancient line, since its ancestors are among the oldest known fossils from the Cambrian. They are now correctly placed in a separate phylum, intermediate between the Annelida and the Arthropoda.

Leaving out the Onychophora, the Arthropoda may be subdivided into the four large major divisions typified in Pl. 1. I (B-G).

(i) The **Trilobites**, which flourished in the primaeval seas, from the Cambrian up to the Permian, that is to say for hundreds of millions of years. Their body was composed of a cephalothorax, an abdomen and a postabdomen. They had only a single pair of antennae, and a long series of paired biramous appendages, all more or less alike. The sides of the body-segments had broad lateral expansions, called '*pleura*', resembling the 'paranotal lobes' of insects to which we shall return later.

(ii) The **Crustacea**, especially abundant in the oceans, but also represented on dry land and in fresh water. The Crustacea have two pairs of antennae, and at least five pairs of legs. In the more advanced forms the body consists of a cephalothorax and an abdomen. Respiration is by gills (branchiae). No Malpighian tubules. Genital ducts opening anteriorly (progoneate).

(iii) The **Cheliceræ**, or **Arachnida**, are characterized by the presence of cheliceræ (pincers) in place of antennae, and have four pairs of legs. The body consists of a cephalothorax and an abdomen. Tracheae are present only in the more advanced forms. Malpighian tubules are present, and the genital ducts open anteriorly (progoneate).

(iv) Finally, the **Antennata**, which have one pair of antennae and a variable number of legs. Respiration is by tracheae, and all groups have Malpighian tubules. The head is always separated from the thorax.

The section Antennata is made up of three Classes, which differ from each other in the mode of growth of the body, and in the position of the genital orifice, which may open either anteriorly or posteriorly on the abdomen.

1. Class *Progoneata*, or Myriapoda in which the genital orifice opens on one of the segments close behind the head. The number of segments in

the body increases during the life of the animal. Symphyla; Pauropoda; Diplopoda.

2. Class *Oplithogoneata*, or Myriapoda in which the genital orifice opens on one of the posterior segments of the abdomen. The number of segments in the body increases during the life of the animal in the majority of the species, but is fixed in some of the more advanced forms. Schizotarsata; Chilopoda.

3. Class *Insecta*, in which the number of segments behind the head is fixed; the body divided into three regions (tagmata): head, thorax, abdomen; and the genital orifice opens posteriorly, as in the Oplithogoneates above.

ORIGIN OF THE INSECTS

The Insects are perhaps the oldest inhabitants of the surface of the continents. They have left fossil traces in the very ancient Palaeozoic deposits (the Devonian of Scotland), and the degree of evolution of these, the first insects known, shows that they must have branched out at the latest by the Silurian. Ever since the animals began to colonize the surface of the lands that had emerged from the sea, that is for 500 million years, insects have swarmed over all the regions of the globe.

Without conclusive proof, we may suggest that the earliest ancestors of the insects must have originated on some swampy tropical shore of a Silurian continent. Since the whole evolution of insects is linked with the evolution of plants, we are justified in assuming that their origin, too, was in some way associated with the Plant Kingdom.

The ancestors of the land plants flourished in the sea: the ancestors of the insects must also have been marine, feeding on marine plants. When the plants spread out of the sea, into the coastal swamps, they were at first restricted to very humid surroundings, then they adapted their respiration little by little to living on dry land, developing stomata on their vegetative parts, long before they had evolved leaves. One can imagine a similar adaptation taking place in the insects. After a long period in which they made do with cutaneous respiration in an atmosphere saturated with moisture, they developed spiracles and tracheae.

In this way the first step in the evolution of the insects after leaving a marine habitat may have been taken in close association with the plants. From such a simple beginning, the association of plants and insects has continued, and has become more and more intimate.

Hypotheses of the Marine Origin of Insects

The question thus arises: what were these marine ancestors of the insects? All kinds of theories have been suggested. Today we no longer

believe that the insects could have arisen directly from Annelida, or from Onychophora. Their progenitors were already true Arthropoda.

This being agreed, the phylogenetic theories about the origin of the Insecta fall into two categories. One group make the insects come directly from marine forebears; the other group of theories derive the insects from a terrestrial ancestor, itself, of course, descended from a marine form, but being a common ancestor to all the tracheate Arthropoda (i.e. Myriapoda and Insecta, which breathe by means of tracheae).

HANDLIRSCH'S Trilobite Theory

Among the theories which derive the Insecta directly from marine ancestors, we must consider first that of Handlirsch, according to which the Insecta arose from Trilobites. The wings of insects would then be homologous with the *paranotal lobes*, broad lateral extensions of the sides of the segments, which are seen in Trilobites. The Trilobites do, in fact, show a number of characters that support this hypothesis. They are older than the Insecta, since they certainly lived in the seas of Precambrian times. They have only a single pair of antennae, like insects, compound eyes, three ocelli, and sometimes anal cerci; their biramous appendages may well have given rise to the more specialized ones we find in insects.

Unfortunately, in order to support his theory, Handlirsch needed to show that the winged insects (Pterygota) were the direct descendants of the Trilobites, and consequently that the wingless insects (e.g. Thysanura) had not appeared ahead of the winged forms, but on the contrary were more recent: in brief, that the Apterygota were Pterygota that had lost their wings by a process of degeneration. This hypothesis, besides being difficult to accept, has been definitely contradicted by fossil evidence, which has shown that the Apterygota are in fact much older than the Pterygota. It follows that Handlirsch's Trilobite Theory has had to be abandoned.

In addition, we now know that the Trilobites are a big, independent Phylum, the Trilobitimorpha, which has particularly close affinities with the Arachnidomorpha. This rules them out of the direct line of ancestry of the Insecta. Again, why should the earliest terrestrial ancestors of the insects have had wings from the beginning? It is much more likely that they crawled about on the ground for a long period, as the Thysanura still do: some of these (*Lepisma*) have preserved down to the present day the paranotal lobes, which have never evolved any further. These lobes became wings only slowly, as the tall plants grew into forests.

Other authors have sought a marine ancestry for the insects among the various groups of Crustacea: Hansen among the Syncarida; Crampton among the Isopoda, the Tanaidacea, the Cumacea.

Theories of BRAUER and of VERLUYS

There are a variety of theories deriving the insects, not directly from a marine ancestor, but from a terrestrial one, and all of them presuppose that the aquatic insects of the present day, living in fresh water, are descended from terrestrial ancestors, and not from marine ones. The adaptation of these insects to an aquatic life is no more than a return to habits that their remote marine ancestors abandoned long ago.

The old theory of Brauer suggested *Scolopendrella* (Symphyla) as this primaeval land insect. Verluys and Demoll would derive all the terrestrial Arthropoda, including the Arachnida, from a hypothetical Myriapod, itself descended from a marine member of the Onychophora.

A more modern approach to this problem is that of Tillyard (1930).

TILLYARD'S Theory

According to this theory, the Insecta and the Myriapoda descended together from hypothetical ancestors, probably in the Silurian period, which he calls *Protaptera*. There is no reason why these unknown Protaptera should not themselves be derived from very primitive Trilobita.

The Protaptera would then divide into two branches, one with the genital duct opening anteriorly on the abdomen (*Progoneata*) and the other with the opening posteriorly (*Opisthogoneata*). The latter would then themselves have split into two branches, which at the present day are represented by the Schizotarsata and Chilopoda on the one hand, and the Insecta on the other.

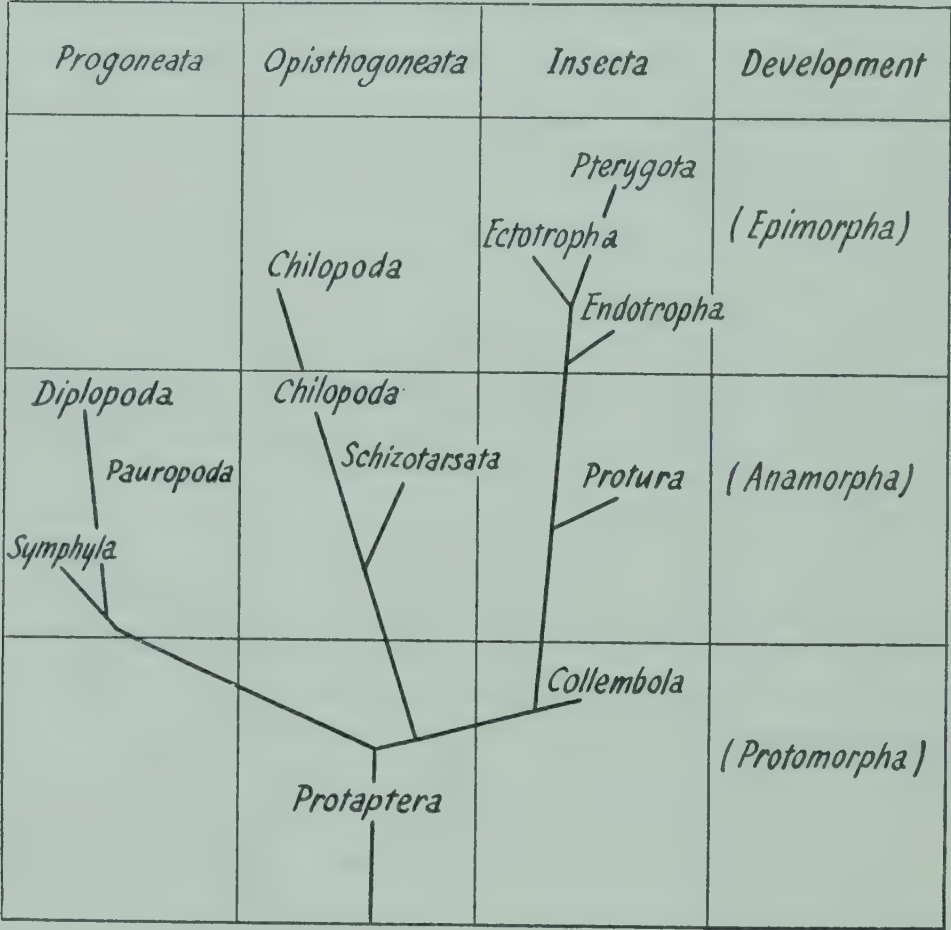
From the Insecta branch there first split off at an early date the Collembola, then the Protura, two groups which possess many characters in common with the Myriapoda. More recently the stem divided again into two: the endotrophic Thysanura (or Diplura) on the one hand, and the ectotrophic Thysanura on the other. The Pterygota may be derived directly from the ectotrophic Thysanura, the wings being a specialized development of the paranotal lobes of the thorax.

The following diagram displays these phylogenetic relationships. It shows, moreover, how the segmentation of the body has developed in parallel fashion in the three Classes: Progoneata; Opisthogoneata and Insects.

Protomorpha are primitive forms still having only a small number of segments in the body: Collembola have only 15 (6 in the head, 3 in the thorax, 6 in the abdomen).

Anamorpha are those forms in which the number of segments after the head increases during the life of the insect, by the subdivision of some of the posterior ones. This subdivision does not stop until the insect has become an adult.

Epimorpha, finally, are those in which the number of segments is fixed for good after the early stages of embryonic development. The more advanced Chilopoda are epimorphic, and so are the higher Insecta. In the latter, as we have seen, the number of segments is fixed at 21 (6 in the head, 3 in the thorax, 12 in the abdomen).



2

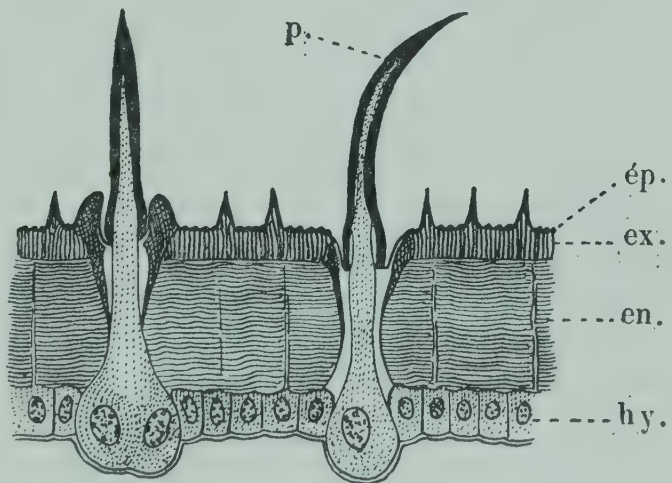
External Morphology

GENERAL STRUCTURE

Size. The biggest insects are the Phasmida (here included in the Orthoptera), whose length approaches 30 centimetres. Among the Coleoptera, *Titanus giganteus* (Cerambycidae) attains 15 cm., and among Lepidoptera, *Erebus agrippina* has a wing-span of about 28 cm. But these giants among living insects compare poorly with those of the Carboniferous period. The insects found at Commentry (Upper Carboniferous) were all of very large size, and certain primitive dragonflies had a wing-span of 70 cm.

The smallest of living insects are of the order of one quarter of a millimetre (TRICHOPTERYGIDAE, among the Coleoptera; MYMARIDAE, egg-parasites, in the Order Hymenoptera, even smaller than the former). As Folsom has pointed out, the smallest insects are smaller than the biggest Protozoa, while the biggest insects are greater than the smallest mammals.

Fig. 1 – Diagrammatic section of the integument of an insect, p, hair; hy, hypodermal layer; en., endocuticle; ép, epicuticle; ex, exocuticle (after WEBER).



THE INTEGUMENT

The integument, or body-wall of insects (Fig. 1) is made up of two layers: beneath is the *hypoderm*, composed of living cells, resting on a basal membrane; above this is the *cuticle*, secreted by the hypodermal cells, and itself divisible into three layers. The deepest of these is the *endocuticle*, or pigmented layer; above this extends the *exocuticle*, formed from excessively thin plates of chitin, whose thickness is of the same order as the

wave-length of light; finally, on top of all is *epicuticle*, a very delicate covering, of varied composition, but not chitinized, no doubt a secretion of the hypodermal glands. In this epicuticular layer have been detected sulphur, potassium nitrate, fatty compounds, and cholesterol; its functions are varied, and include excretion, general protection (e.g. the hydrofuge secretions of aquatic insects), or mere ornament (e.g. the solid colouring-matter of the weevils).

Sclerites and membranes. The integument of insects is more or less stiffened. In certain beetles (e.g. *Dicerca*, *Cleonus*, *Brachycerus*) it is hardened to such an extent that sometimes the entomologist has to punch a hole to prepare a way for the entomological pin on which the specimen is to be mounted. The areas of sclerotization are joined by membranous folds, and the sclerites themselves are more often a secondary development than a part of the primitive segmentation of the insect's body.

The meeting of two sclerites is visible as a *suture*, but there are other sutures to be seen on the surface of the sclerites which are produced in a different way. These generally correspond to *apodemes*, which are folds of the integument drawn inwards to act as anchorages for muscles. The apodemes are collectively known as the *endoskeleton*.

The membranous areas of the integument are those in which the cuticle remains supple, and is not sclerotized. Although a beetle, for example, may seem to have few such areas, in fact the total extent of membranous integument is considerable, often more than half of the whole; the membrane is mostly folded, and concealed beneath the overlapping sclerites. Enormous areas of membrane lie hidden in the folds of the neck region, between the prothorax and mesothorax, between the sclerites of the abdomen, and under the elytra.

These membranous areas often function as respiratory surfaces, as in the sub-elytral chamber of many cave-dwelling beetles. They also make possible the inhaling and exhaling movements that cause air to circulate in the tracheae. Again, they permit a distension of the abdomen, which is often considerable, as a result of the accumulation of fat-body, or of food-material in the gut. This reaches an extreme in the physogastric termites, which become little more than a storage-sac.

Pigmentation. Brown or black colours, greens and reds, are produced by pigments formed in the endocuticle, in the hypodermal layer, or even in the organs immediately below the integument. If their pigment is destroyed, insects appear testaceous, that is pale yellow, or a little reddish, which is the natural colour of chitin.

Metallic colours, on the other hand, are physical colours, caused by interference among the light-rays which penetrate the thin layers of the exocuticle, seen against the black background of the deeper layers. These colours are dependent upon the exact spacing of the layers, and so are

easily destroyed. The golden colour of the CASSIDINAE (Coleoptera: CHRYSOMELIDAE) disappears after death, but that of *Plusiotis* (RUTELIDAE) persists in dried specimens.

The extent of the coloured pattern in insects is correlated with the conditions of their habitat. Species living in deep water are generally without pigment, or with irregular dark markings. Melanic forms, which occur at high altitudes in the mountains, are especially common in metallic species. No doubt they are caused by modification of the thickness of the layers of the exocuticle, which may be affected by the degree of humidity, but the conditions which bring about these melanistic variations are not yet fully understood.



Fig. 2 - Some types of dermal structures. A, B, C, fringed and barbed hairs of Hymenoptera; D, adhesive hairs from the tarsus of a Carabid beetle; E, abdominal scales of Hymenoptera.

Microsculpture. Much use has been made in systematics of the polygonal alutaceous network that covers the integument of insects. Whenever this network is highly developed it produces a matt appearance. It has no connexion with the *puncturation*, which is produced by the pits in which hairs are inserted.

The alutaceous network marks out the areas of chitin deposited by the hypodermal cells. Its development seems to be related to the humidity of the insects' surroundings. The shape of the polygons is variable, and helps to characterize species.

Cuticular processes. Under this term we include all the structures that arise out of the surface of the integument, and we may divide them into two groups.

The *fixed processes* may take the form of teeth, large or small, rows of teeth (crenellations), or swellings (tubercles); on a bigger scale they

may become apophyses, or even horn-like extensions, simple or branched, which may be elaborately developed.

The *movable processes* (Fig. 2) are the hairs. On the one hand they may form a pubescence of greater or lesser extent; on the other they may remain isolated and individually developed. Some groups of insects are clothed with scales, which are modified hairs (Lepidoptera; some Coleoptera—CURCULIONIDAE).

Bristles (setae or macrochaetae) is the name given to single hairs which have a definite, specialized form, and which occupy a precise position on the body. The study of these bristles (chaetotaxy) is very important in the systematics of certain groups (Diptera). These bristles may also have a peculiar structure (the whip-like sensory setae of Adephaga, the trichobothria of Orthoptera).

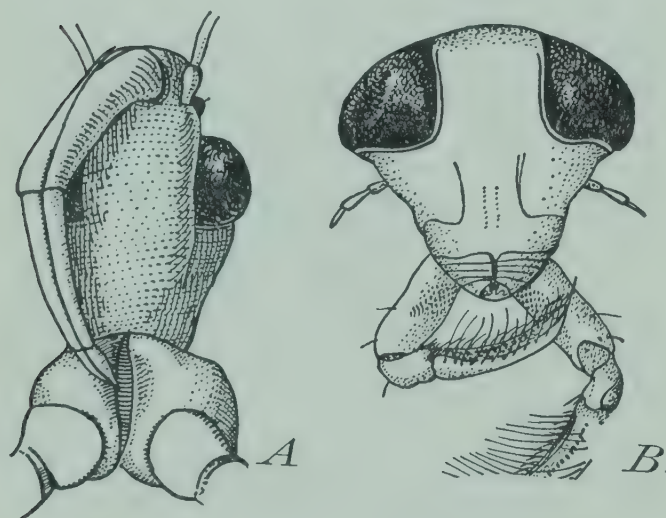


Fig. 3 – Stridulatory organs of two Hemiptera. A, *Coranus subapterus* (Reduviidae), the tip of the Rostrum rubbing against ridges in a groove of the sternum; B, *Corixa geoffroyi* (a water-bug), the tarsus of the fore-leg rubbing against the bases of the femora, and the ventral face of the head (after WEBER).

Stridulating organs. Many insects are able to make sounds by rubbing together parts of the body. Such stridulating organs are always developed by the mutual adaptation of two adjoining parts of the body, of which one (the *pars stridens*) is fixed, and has small, transverse, toothed ridges; the other member (the *plectrum*) is roughened, and rubs on the *pars stridens* like a bow on a violin.

Stridulating organs are found in the most diverse groups of insects, and in either males or females. They may occur in different regions of the body, without any correlation with the systematic grouping of the insects concerned (Fig. 3). There is no space here to list all the different pairs of stridulating organs that occur in the various Orders of insects and especially in the Orthoptera and Coleoptera. It may be said that nearly any part of the body that makes contact with some other part might, given the evolutionary stimulus, be adapted as a stridulating organ.

THE HEAD

The head of an insect is a more or less completely sclerotized capsule, with two openings: the mouth, and the neck opening (*occipital foramen*). It is formed by the coalescence of six primitive segments, of which traces can usually be detected in the adult insect: they can always be seen in

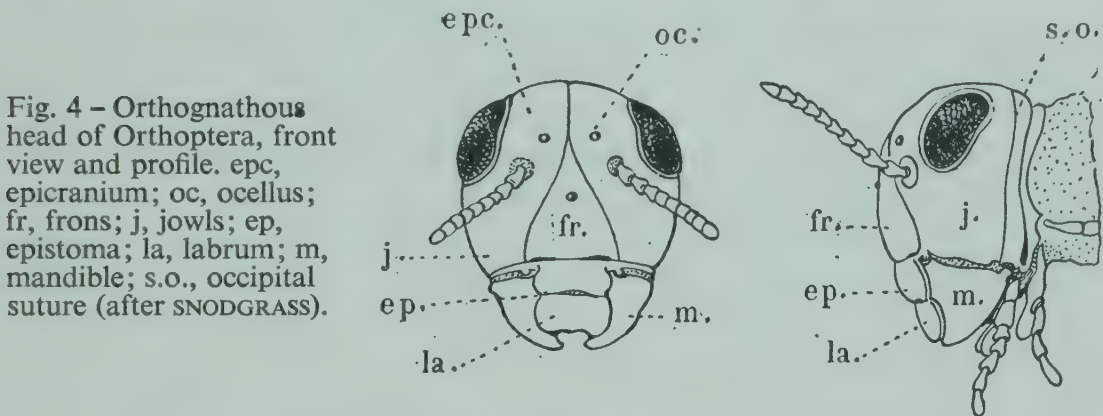


Fig. 4 – Orthognathous head of Orthoptera, front view and profile. epc, epicranium; oc, ocellus; fr, frons; j, jowls; ep, epistoma; la, labrum; m, mandible; s.o., occipital suture (after SNODGRASS).

embryonic insects. The antennae, and the mouthparts (mandibles, maxillae and labial structures) are the paired appendages of the second, fourth, fifth and sixth primitive segments.

The cranium. The cranium of an insect is made up from a certain number of sclerites, divided by sutural lines which bear no direct relation to the primitive segmentation.

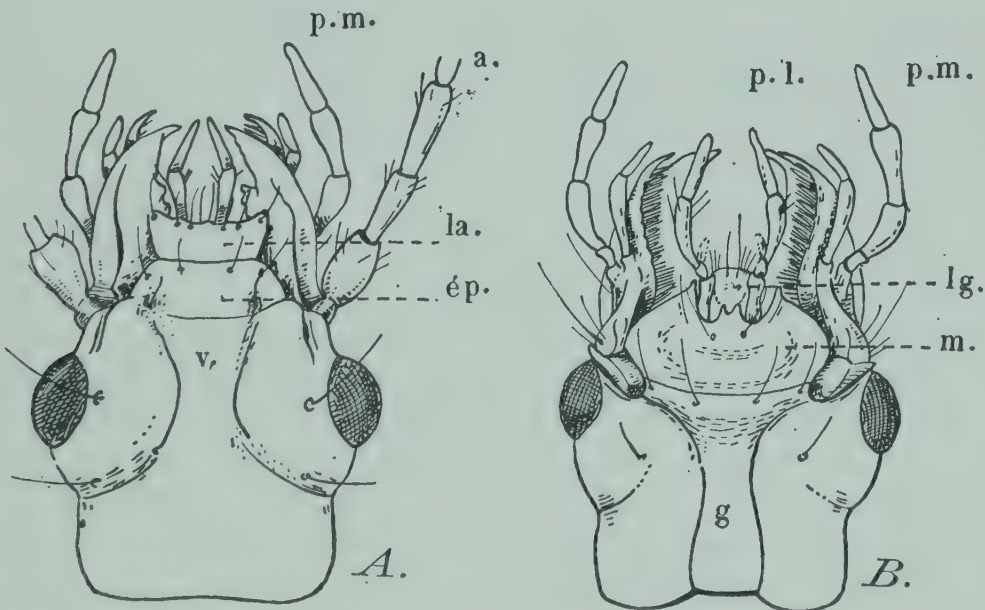


Fig. 5 – Prognathous head of a *Trechus* (Carabidae): A, dorsal view; B, ventral view; v, vertex; ep, epistoma; la, labrum; a, antenna; p.m., maxillary palp; p.l., labial palp; lg, ligula; m, mentum; g, gula (after JEANNEL).

The epicranium comprises all the dorsal and lateral areas of the head, and can be divided into regions: vertex (Fig. 5 v); jowls or buccae (Fig. 4 j), and occiput (Fig. 4 s.o.). In larvae, and in many adult insects the

epicranium is symmetrically divided into two halves by a longitudinal suture known as the 'coronal suture'. Anteriorly, this suture is forked into two 'frontal sutures', between which is the *frons*. While the epicranium provides a great surface for the attachment of the antennary and mandibular muscles, the frons roofs over the cerebral ganglia.

Anteriorly, the frons is divided from the *epistoma*, or clypeus, beneath which is the pharynx. The anterior margin of the epistoma articulates with the *labrum* (Fig. 5 *la*), which constitutes the upper lip of the mouth, and which has on its internal surface organs of taste—papillae, hairs, bundles of spines—which are collectively termed the *epipharynx*.

The *gula*, or ventral sclerite, is a plate which occupies the ventral surface of the head capsule, along the middle line. It is not always present, but when it occurs, its anterior margin articulates with the *mentum* or *submentum* of the labium.

The epicranium, of which we have given a brief description, is the exoskeleton of the head. There is also an endoskeleton, known as the **tentorium**. This is an arrangement of chitinized arches, criss-crossing between the two sides of the head, and dividing it up into compartments. These arches serve as attachments for muscles, and represent the remains of the invaginated maxillary segment. Externally, the insertions of the 'wings' of the tentorium define the limits of the epistoma; those of the 'pillars' of the tentorium appear ventrally on each side of the gula.

Whenever the mouth-opening is turned towards the ventral, perpendicular to the axis of the body, as it is in the locust (Fig. 4), the head is said to be *orthognathous*: this is the primitive type. But often the mouth has become displaced towards the anterior part of the head, and is now terminal (Fig. 5): in this *prognathous* type the pull exerted by the mouth-parts has led to the displacement forwards of the points of insertion of the pillars of the tentorium, and thus the gula is elongate. In contrast to this, it sometimes happens that the mouth has become displaced not forwards, but backwards on the head; this is the case in the Homoptera-Sternorrhyncha, in which the proboscis seems to come out from between the fore coxae, and in these groups the mouth is said to be *hypognathous*.

The eyes. The eyes of insects vary a great deal in construction and in degree of complication. Nevertheless, we can group them into two categories, simple eyes and compound eyes.

Simple Eyes

There are two kinds of simple eyes:

(i) *Stemmata* are lateral in position on the head, situated on the sides of the epicranium, posterior to the antennae. Such are the eyes of larvae. All stages exist between the simple pigmented spot, without a specialized cornea, found in Culicid larvae, and the advanced stemmata of a Cicin-

delid larva, with thick cornea, pigment, rhabdome, and numerous sensory cells.

(ii) *Ocelli* have very nearly the same structure, but are median in position. The maximum number is three: one on the frons, two on the epicranium (Fig. 4). *Ocelli* are especially characteristic of adult insects, and are mainly found in primitive groups.

Compound Eyes

These are characteristically the lateral eyes of adult insects, replacing the stemmata of the larva, and occupying a similar place on the head. They are distinguished by the presence of a layer of nerve-tissue below the retinal cells, and by a complex assembly of optical units or *ommatidia*, or simple eyes. These latter vary greatly in number, and there may be up to tens of thousands of them, each with its facet.

We have already mentioned a peculiar kind of compound eye, which may occur in COCCIDAE and Strepsiptera, and which is an aggregation of stemmata rather than a true compound eye.

Double compound eyes occur in *Simulium* and *Bibio* (Diptera), and in the GYRINIDAE (Coleoptera): the two parts of the eye are different in structure, and no doubt also in their operation.

The antennae. The antennae of all insects are composed of three sections: scape, pedicel and flagellum.

The *scape* is the basal segment, and articulates by means of a ball-joint (scapobasal) upon a projection (antennifer) of the epicranium. The scape is moved by elevator and depressor muscles attached to the cranium, and has its own muscles which operate the next segment, the pedicel.

The *pedicel*, or second segment, is generally short, and its main importance is that it bears a sensory organ called Johnston's organ.

The rest of the antenna after the pedicel is called the *flagellum*. The number of segments in this region varies from a single one in beetle larvae up to 60 segments in some adult CERAMBYCIDAE (Coleoptera). Most often the number of flagellar segments is nine.

Variation in Form and Structure

Antennal characters are of the greatest importance in classification of insects, and there is great diversity (Figs. 6 and 7).

The most primitive antenna is considered to be that in which the flagellum is made up of a large number of similar segments, which gradually diminish towards the tip. These segments may be bare, or may have whorls of hairs, or sometimes may be feathered. A 'filiform' antenna is one in which the segments are elongate and cylindrical; a 'moniliform' one is made up of short, rounded segments, like a string of pearls. Occasionally

the antenna is elbowed, with the scape elongate, and the pedicel and flagellum set at an angle to it.

When the flagellar segments are asymmetrical we have all stages between the serrate and the pectinate (Fig. 6, *C, D*); if the projections are on both sides we get 'flabellate' antennae.

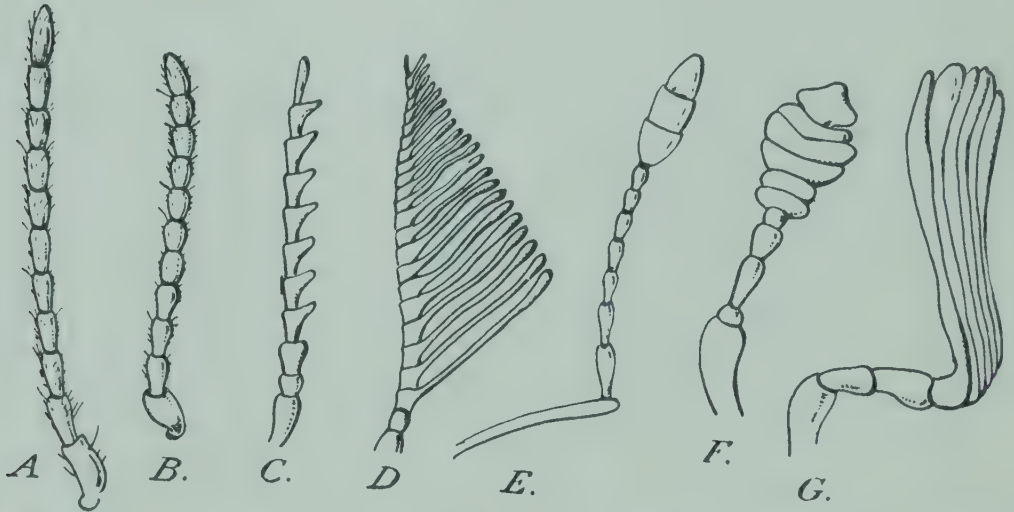


Fig. 6 - Various types of antenna. A, filiform; B, moniliform; C, serrate; D, pectinate; E, elbowed and capitate; F, capitate; G, lamellate.

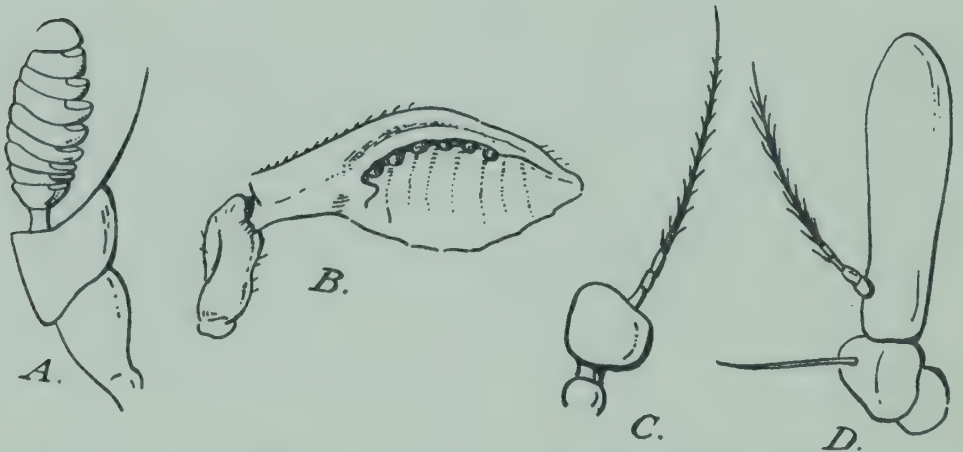


Fig. 7 - Various types of antenna. A, clubbed capitate of a flea (Aphaniptera); B, antenna of *Paussus favieri* (Coleoptera); C, aristate antenna of *Phora* (Diptera); D, aristate antenna of *Melophagus* (Diptera).

The capitate antenna has the distal segments of the flagellum swollen compared with those nearer the base; the flagellum is then in two parts, the slender stalk (or funicle) and the head. The head may be compact, with the segments grading smoothly one into another, but sometimes it is uneven in outline (CATOPIDAE, HYDRAENIDAE), and then it is the eighth segment that is smaller than either the seventh or the ninth, which are

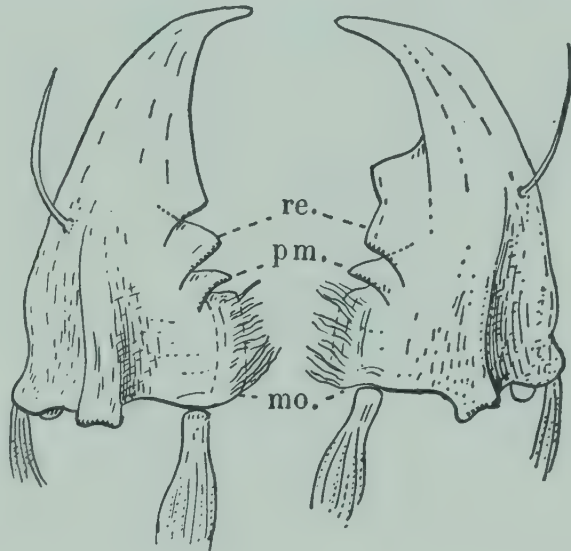
dilated and bear blister-like olfactory sense organs. Asymmetrical capitate antennae result in the 'lamellate' antennae of *Lamellicornia* (Fig. 6, *G*).

The *Diptera-Brachycera* have a very specialized kind of antenna, with an 'arista', and among the myrmecophilous *Coleoptera* (*Paussus*; *Ptinus*) there are antennae that are curiously modified by the fusion and swelling of the segments of the flagellum (Fig. 7). In *Dahomey* there are even *Paussus* in which the antennal flagellum is transformed into a luminous sphere.

Special mention must be made of antennae that are used for respiration. In *Hydrophilids*, *Gyrinids*, *Dryopids*, and also in those *Platypsyllus* that live in the fur of beavers and consequently are often under water, the pedicel of the antennae takes the form of a cup and a lid, and is used to trap a bubble of air at the surface and thereby to replenish the air-reservoir stored among the hydrofuge hairs on the venter of the body.

The mouthparts. First of all we must consider the chewing type of

Fig. 8 - Mandibles of *Aepopsis robini* (Carabid beetle). re, retinacula; pm, premolar tooth; mo, mola (after JEANNEL).



mouthparts, which is certainly the most primitive, and which helps us to understand the more complicated structure of the licking, sucking and biting types found in other insects.

Chewing Mouthparts

These are found in the lower insects: *Thysanura*, *Orthoptera*, *Odonata*, *Plecoptera*, and also in many of the higher groups of insects such as *Coleoptera*, certain *Hymenoptera*, and the larvae of *Lepidoptera* and *Trichoptera*. A set of chewing mouthparts includes paired components (mandibles, maxillae, and the double labium) and unpaired components (labrum and hypopharynx).

Mandibles. The mandibles of *Thysanura* are like those of *Myriapods*, being elongate, and articulated to the cranium by a single condyle. In the

Pterygota the mandible is shortened, broadened at its base, and has developed a second articulation (Fig. 8). This secondary articulation is dorsal. The mandible generally moves about a dorso-ventral axis, slightly oblique, so that the points of the mandibles move slightly downwards as they come together. This axis is orientated differently in the CURCULIONIDAE. In *Balaninus* the mandibles move vertically (i.e. about a horizontal axis), and there are even groups of CALANDRINI in which the axis of rotation is so displaced that the mandibles work outwards and away from each other, instead of inwards and together.

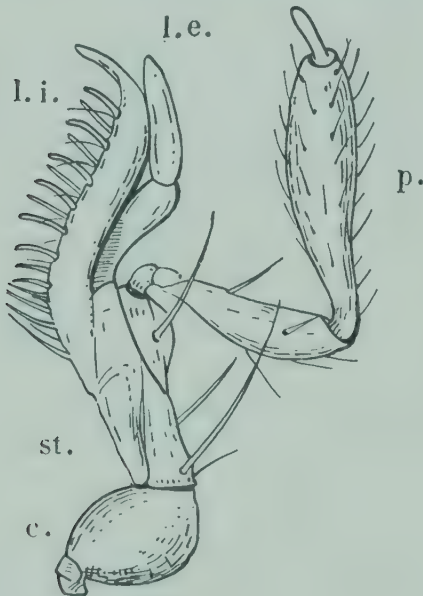


Fig. 9 – Left maxilla of *Porotachys bisulcatus* (Bembidiidae) seen from the ventral face. c, cardo; st, stipes; l.i, internal lobe; l.e, external lobe; p, palp (after JEANNEL).

Mandibles of the chewing type do not vary greatly. They are roughly in the form of triangular pyramids, a little flattened, with three faces (dorsal, ventral and external); three edges of which one forms the inner, masticating edge; a triangular base; and a point that is more or less incurved.

The proximal part of the inner edge is most often thickened, folded or tuberculate, and is called the *mola*. In front of the mola the edge may have either teeth or mobile attachments (*lacinia mobilis*, *prostheca*). The point of the mandible (*terebra*) often has many teeth, and between this point and the mola and accessory tooth (the *retinacula*) often occurs. Finally, between the retinacula and the mola there is sometimes yet another tooth, the *premola*.

The mandible of insects never bears a palp comparable with that of Crustacea, but this structure is no doubt represented in insects by a bristle that is often present on the external face.

Certain weevils show a curious evolution of the mandibles. The points of the mandibles of OTIORRHYNCHIDAE grow large during the pupal stage, and then are shed shortly after emergence of the adult.

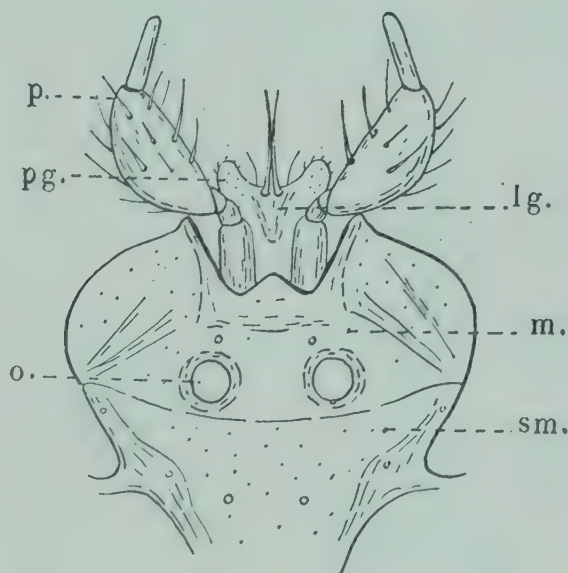
Maxillae. The maxillae (Fig. 9) consist of three segments (*cardo*, *eustipes*, *costipes*), of which the last two bear lobes, and a palp, which represents the endopodite of the Crustacean appendage.

The basal segment, the *cardo* articulates by means of a single condyle with the anterior part of the pillar of the tentorium. The two segments that make up the *stipes* (*eustipes* and *costipes*) are not always clearly separated; they are fused in the Orthoptera, but visible in the Coleoptera (Fig. 9). The *eustipes* extends internally as a mobile maxillary blade or lamella, the *lacinia*, which is spiny or fringed with hairs; the *costipes*, or palpiger bears the *galea* and the palp that we have already mentioned. The *galea* sometimes has numerous segments; and in certain Coleoptera (*Adephaga*, or *Hexapalpata*), it has all the appearance of a palp. The *lacinia* and the *galea* are sometimes referred to as the internal lobe and the external lobe, respectively.

The maxillary palp has five segments in the cockroaches, seven in *Agrion*, and four in Coleoptera. It can be shown that the palp has subdivisions corresponding to those of a true walking leg, which is also a segmental appendage.

Labium—The labium (Fig. 10) is the result of the fusion of the second pair of maxillae into one organ: its basal part has absorbed, in addition, a part of the labial somite, with the result that its structure is complicated.

Fig. 10 - Labial structures of *Porotachys bisulcatus* (Bembiidae), seen from the ventral face. sm, submentum; m, mentum; pg, paraglossae; p, palp; o, labial sensory organ (after JEANNEL).



Two parts may be recognized in the labium: the proximal, or *postlabium*, corresponding to the two cardines fused with the labial sternite; and the distal, or *prelabium*, composed of the stipites and their lobes.

The submentum, or anterior margin of the gula, carries a broad, usually mobile piece, which is generally called the 'labium': this is really a part of the postlabium, being homologous with the cardines of the maxillae, and is nowadays usually called the *mentum* (Snodgrass).

The prelabium, corresponding to the stipites, is represented by a *prementum* in the Orthoptera and certain Coleoptera (ALEOCHARIDAE). This part of the labial structures is membranous and hidden behind the mentum in the CARABIDAE and related Coleoptera. The lobes are represented by a little tongue, or ligula (lacinia) and by the paraglossae (galea). The labial palpi always have one or two segments fewer than the maxillary palpi.

Labrum and hypopharynx. We have seen that the *labrum* is an upper lip, whose inner face, or epipharynx covers the mouth. On the opposite, or ventral side of the mouth, the mentum forms a lower lip, and conceals a folded, membranous organ called the *hypopharynx*, which is equipped with taste-cells, and with paired lobes, which are sometimes chitinized and articulated. These last have been claimed as vestiges of a third pair of mandibles, but the embryonic development shows this to be false.

Often there are salivary glands opening at the base of the hypopharynx.

A curious specialization of chewing mouthparts is seen in the aquatic nymphs of dragonflies. Here the labial structures are greatly drawn out, and developed into a prehensile organ, the *mask*. At rest, this organ is folded beneath the body, but it can be shot out suddenly to seize prey and convey it to the mouth. Pl. 1, II (A). A device that is similar, but even longer, is found in the small riparian STAPHYLINIDAE of the genus *Stenus*. In the dragonfly nymph the jaws of the pincers are the labial palpi, but in *Stenus* they are the paraglossae.

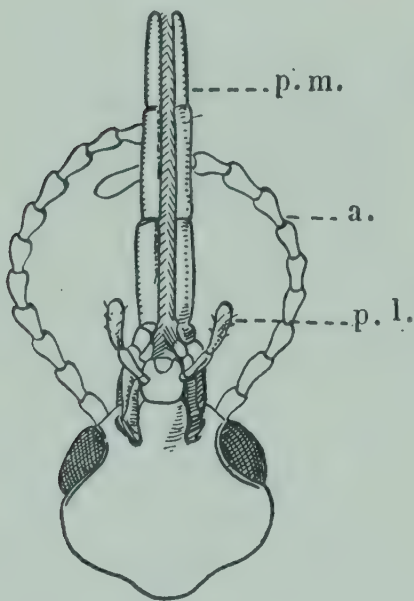


Fig. 11 - Head of *Leptopalpus* (Meloïdae), ventral aspect, showing the proboscis built up from the two ciliated maxillary lobes pressed together. a, antenna; p.m., maxillary palp; p.l., labial palp (after WEBER).

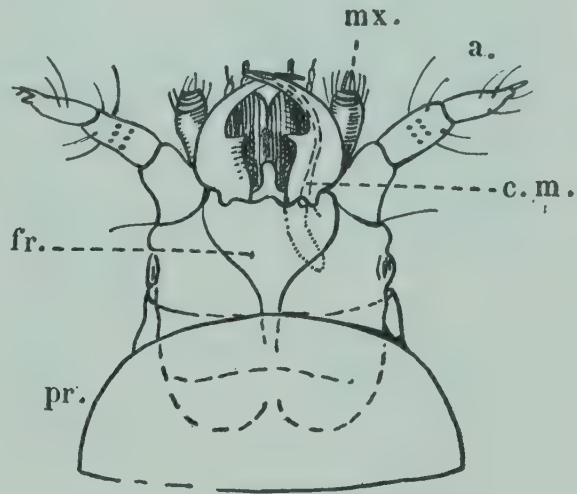
Licking and Sucking Type of Mouthparts

In certain flower-feeding Coleoptera (*Leptopalpus*), the galeae of the maxillae, placed one on top of the other, and reinforced by the palpi,

form a long proboscis by means of which the insect sucks nectar from flowers with a deep corolla. (Fig. 11.)

A variety of insects have the mouthparts adapted in this way for taking up liquid food. In all of them, the licking and sucking type of mouthparts is characterized by the fact that the mandibles do not enter into the

Fig. 12 – Head of the larva of *Lampyrus noctiluca* (glow-worm), showing the mandibular canal. pr, prothorax; fr, frons; c.m., mandibular canal; a, antenna; mx, maxilla (after VOGEL).



formation of the proboscis; they either remain as organs for seizing food, as in the Hymenoptera, or they atrophy and disappear.

The Honey Bee has normal mandibles, and a sucking proboscis made up of three lobes, the maxillae forming the outer pair, and the labium the median one. Pl. 1, II (B).

The caddis flies (Trichoptera) have a short proboscis, Pl. 1, II (C), which is principally the labium, covered over with an elongate labrum; the mandibles are lost. This proboscis of the Trichoptera represents an evolutionary stage towards the Lepidoptera, Pl. 1, II (D), in which the long, coiled proboscis is a tube produced by the pressing together of the two maxillary galeae; the maxilla itself and its palp are more or less atrophied, along with the labrum and mandibles.

It is known that the uncoiling of the proboscis is a reflex action brought about when a sensation of taste is received by the feet; it can be induced by touching the tarsus of a butterfly with a brush dipped in sugar solution.

Piercing Mouthparts

Here the piercing organs are the mandibles and often also the maxillae, which penetrate the tissues of animals or plants in order to allow the juices to be sucked up.

The head of *Panorpa* or *Bittacus* (Mecoptera) is equipped with a long beak at the end of which sharp mandibles are associated with a short labial proboscis. Pl. 1, II (E).

A curious piercing type is found in some Coleoptera. The aquatic

PLATE 1 – II. MOUTHPARTS OF INSECTS (after WEBER)

A. Larva of **Aeschna** (Odonata). Chewing type. The labium is developed into a jointed prehensile organ, the 'mask', which the insect can shoot forwards to seize prey and convey it back to the mouth.

B. Proboscis of a worker bee (**Apis mellifica**) (Hymenoptera), seen from the front; it is composed of the maxillae and labium only (licking and sucking type).

C. Head of an adult caddis-fly (Trichoptera). Licking type, rather primitive.

D. Head of **Deilephila euphorbiae** (Lepidoptera; Sphingidae). Licking and sucking type. The coiled proboscis is derived from the galeae of the maxillae.

E. Head of **Panorpa communis** (Mecoptera). The head is drawn out into a long beak, at the tip of which the sharp mandibles are associated with a short labial proboscis (a specialized piercing type).

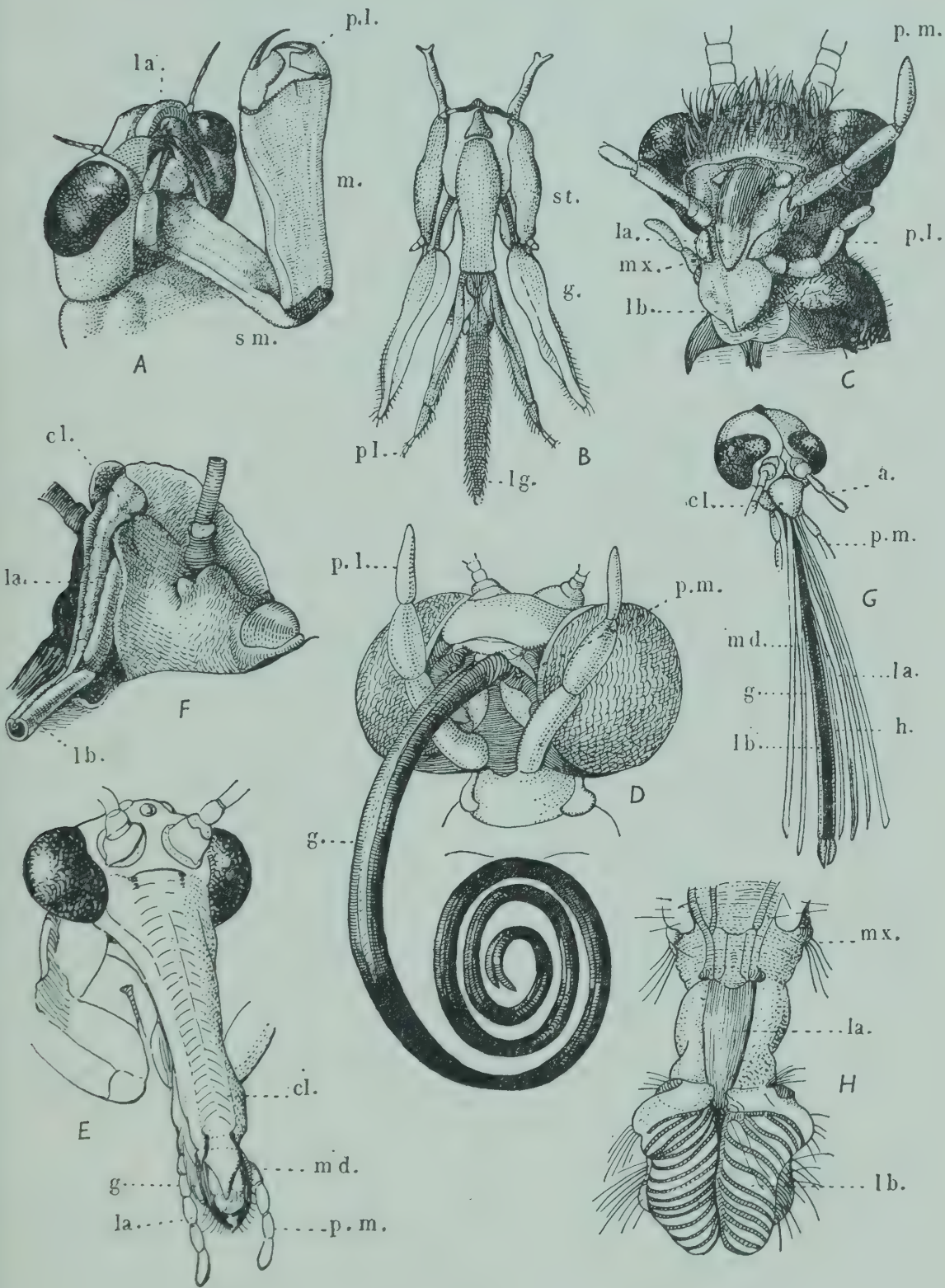
F. Head of **Palomena prasina** (Heteroptera; Pentatomidae). Piercing type, showing the base of the proboscis.

G. Head of female **Culex** (Diptera; Culicidae). Piercing type with six slender stylets ensheathed in a labial groove.

H. Proboscis of **Musca domestica** (Diptera; Muscidae). A licking type, derived from a piercing one by loss of the stylets, and development of the labium.

a, antenna; cl, clypeus; la, labrum; md, mandible; mx, maxilla; g, galea of maxilla; p.m., maxillary palp; lb, labium; p.l., labial palp; h, hypopharynx; lg, 'tongue'; sm, submentum; m, mentum.

PLATE 1-II. MOUTHPARTS OF INSECTS (after WEBER)



larvae of the DYTISCIDAE and the GYRINIDAE, and the terrestrial larvae of *Lampyris* (Fig. 12), which attacks snails have long, sickle-shaped mandibles, pierced by a canal through which the larvae can alternatively inject poison and saliva into its prey, and then suck up the products of this extra-oral digestion. The larva of the Ant-Lion (*Planipennia*), at the bottom of its pit in the sand, also applies external digestion to the prey that it has seized in its long mandibles; but here the suction channel is formed by the maxilla being applied to a groove in the mandible.

The proboscis of the Hemiptera, Pl. 1, II (F), is a highly developed organ, composed of four piercing stylets (the two mandibles and the two maxillae), ensheathed in the labium. In addition there is usually a true suction and compression pump, complete with piston, cylinder and valves, which injects toxic saliva into the prey. In the phytophagous groups, and especially in the PSYLLIDAE, the stylets are coiled up inside the body of the insects in such a way that they can be extended to a length that is sometimes much greater than that of the whole body.

The Anoplura (lice) and the Thysanoptera (thrips) have a proboscis of the same type as that of the Hemiptera, but different in detail. In Diptera, too, we again find the same principle of piercing stylets ensheathed in the labium, but in many groups of flies the stylets have been reduced or lost, and the proboscis is developed for licking and sucking instead of piercing.

The proboscis of the female mosquito, Pl. 1, II (G), has six piercing stylets: the two mandibles and two maxillae, and, in addition, the unpaired labrum and hypopharynx. The whole group is ensheathed in the labium. The same components, but thicker and shorter, are found in the horse flies (TABANIDAE). In *Stomoxys* the mandibles and maxillae have vanished, and the piercing proboscis consists of the labrum and hypopharynx only, with the labium still acting as a sheath. We can trace the same components again in the proboscis of the house fly (*Musca domestica*), but in this insect the labium has been greatly enlarged; the two reduced stylets no longer function as piercing organs, and the labial sponge alone is used to mop up fluids from the surface of surrounding objects.

The proboscis of the fleas (Aphaniptera) recalls that of the Diptera, with some modification.

THE THORAX

The thorax of insects consists of three segments, which Audouin (1824) first called prothorax, mesothorax and metathorax. Some modern authors contrast the prothorax (without wings) with the pterothorax (or wing-bearing thorax), which comprises the mesothorax and metathorax together.

The prothorax is very unequally developed in different groups of insects. In the Orthoptera, Coleoptera, Neuroptera and Hemiptera it is

a complete ring, large and shield-like, but it shrinks and tends to disappear in Hymenoptera and in most of the Mecopteroid Orders.

The neck. The membrane that joins the head to the prothorax is not a simple intersegmental one, but has been proved to incorporate a part of the prothorax and also a part of the labial somite of the head. In addition a whole series of *cervical sclerites* have made their appearance in the membrane of the neck region, and have muscles attached to them. They are specially prominent in the cockroaches.

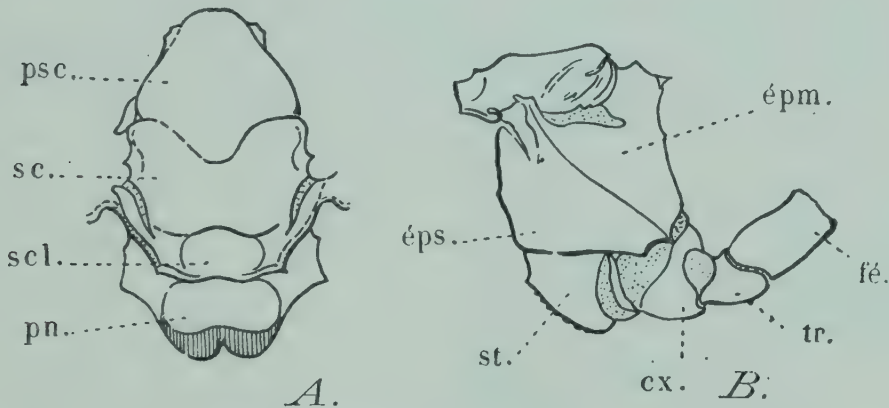


Fig. 13 – Thorax in Hymenoptera: A, mesothorax, dorsal view; B, metathorax, lateral view; psc, prescutum; sc, scutum; scl, scutellum; pn, postnotum; éps, episternum; épm, epimeron; st, sternum; cx, coxa; tr, trochanter; fé, femur (after IMMS).

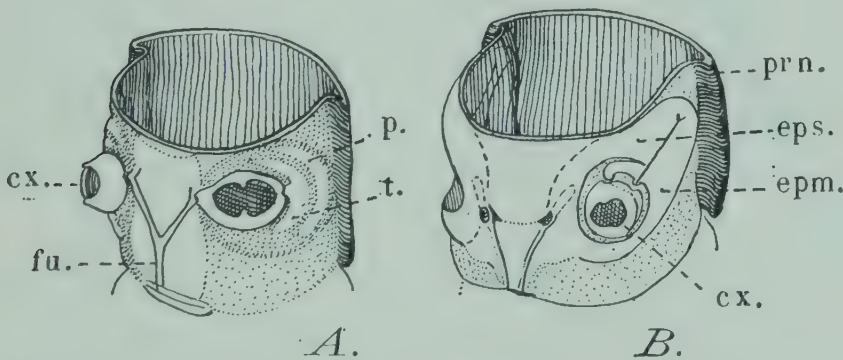


Fig. 14 – Diagram of a thoracic segment of an insect: A, thoracic segment of an Apterygote; B, prothorax of a Pterygote. p, pleura; t, trochantin; prn, paranotal expansion; eps, episternum and trochantin; epm, epimeron; cx, coxa; fu, furca (after WEBER).

Tergites. In many larval insects, and in the adults of the primitively wingless groups (Apterygota), the tergites of the thorax are simple, but the pterothorax of winged insects (Pterygota) has a more complex series of sclerites dorsally. These are collectively known as the *notum*, and as the pronotum, mesonotum and metanotum respectively according to the segment involved. Each segmental notum is further divided into prescutum,

scutum and scutellum, and behind each notum there is a postnotum (sometimes called postscutellum). (Fig. 13 *A*.) The scuta arose from the primitive *paranotal lobes* (Fig. 14), which also gave rise to the wings. In *Lepidoptera* the pronotum also has two lateral lobes, called *patagia*, which no doubt are homologous with the *paranotal lobes*.

Sternites. The ventral plates, or sternites, also divide into presternum, sternum and sternellum. Most of the time, however, only the sternum and sternellum can be distinguished, separated from each other by a transverse suture which marks the position of a big apodeme of the endoskeleton, the *furca*, which carries important muscle-attachments (Fig. 14).

Pleurites. The sternum is extended laterally into two plates, the pre-coxal anterior to the coxal cavity, and the postcoxal behind it, but these

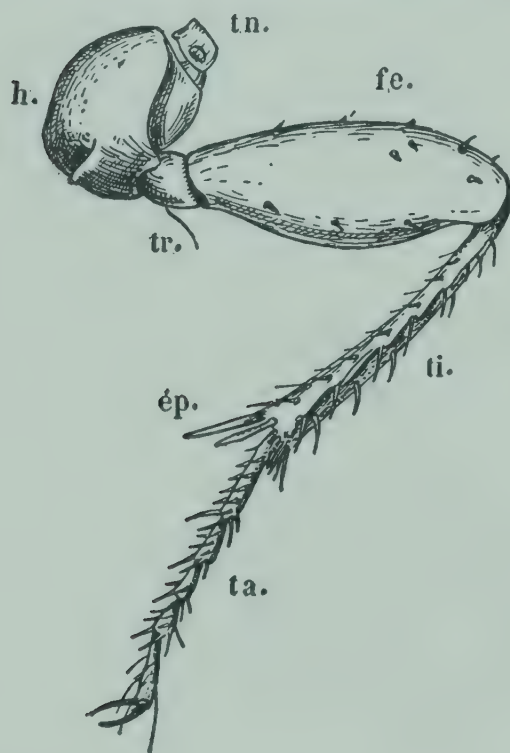


Fig. 15 – Anterior surface of left middle leg of *Trechus bordei* (Coleoptera): h, coxa; tn, trochantin; tr, trochanter; fe, femur; ti, tibia; ép, tibial spur; ta, tarsus (after JEANNEL).

two plates have disappeared in a great many insects. The pleurites proper, extending upwards, away from the coxal cavities, are grouped into the episternum and the epimeron, which are separated from each other by the pleural suture (Fig. 13 *B*).

The episternum and epimeron, and another very small piece, the trochantin, which is often absent, really represent a basal segment of the leg, the subcoxa, which has become incorporated into the thorax.

THE LEGS

These comprise the following segments: coxa; trochanter; femur; medius; tibia; tarsus; and empodium. (Fig. 15.)

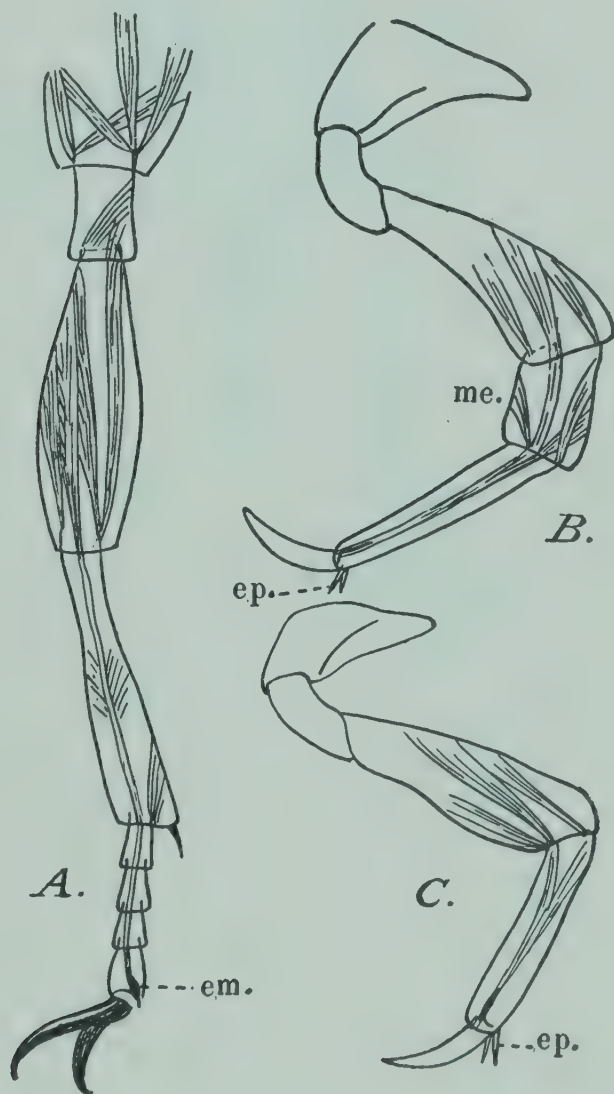
Coxa, or hip. The coxa has several points of articulation with the

thorax. Between the base of the coxa and the episternum is a small articular sclerite, called the trochantin, which is usually considered to be derived from the episternum.

Coxae are very variable in form, and may be globular, conical, flattened, or transverse (i.e. set across the axis of the body).

Trochanter. This second segment of the insect leg is homologous with the basal segment of the Crustacean. Generally the trochanter has a movable joint with the coxa, but a fixed attachment to the femur.

Fig. 16 - Legs of beetles (diagrammatic): A, adult; B, larva of *Adephaga* (six segments); C, larva of *Polyphaga* (five segments); me, medius; em, empodium of adult, corresponding to larval claw; ep, epitarsal spines of the larva, corresponding to the claws of the adult (after JEANNEL).



In Odonata, larvae of DYTISCIDAE, and in some other insects, the trochanter is double; on the other hand, the parasitic Hymenoptera have another trochanter which is a secondary subdivision of the femur. In Strepsiptera, the first two pairs of legs have no true trochanter, but there is a secondary trochanter, fused with the head of the femur.

Femur. The femur is always elongate, and often bears traces of four longitudinal rows of spines, bristles or hairs. Many species have swollen

femora, which sometimes are obviously adapted to jumping, as in grasshoppers, sometimes are secondary sexual characters, as in *Oedemera* (Coleoptera), and sometimes seem to be nothing more than hypertely, or evolutionary exuberance, as in *Sagra* (Coleoptera).

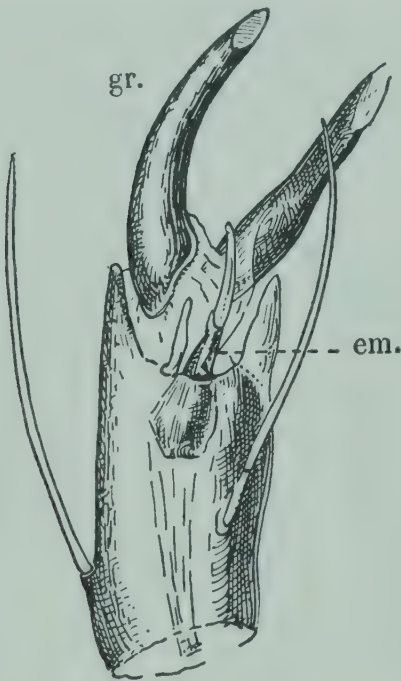


Fig. 17 – Onychium of *Trechus* showing the empodium, with its unpaired structure. gr, claws; em, empodium (after JEANNEL).

Medius and tibia. The tibiae have retained traces of the primitive longitudinal rows of spines even more clearly than the femora. The base of the tibia is pulley-like, and turns between two condyles of the femur. This ‘knee’ in insects, which Börner and Hansen considered to be a primitive articulation, is actually a secondary one. The primitive form of joint in insects is a simple hinge; a joint like that of the knee, with two condyles, is a complex one, and everything points to the disappearance of one segment of the primitive leg. The name ‘medius’ has been given to this missing segment (Jeannel, 1925). It is homologous with the patella of the Arachnids, and represents the ‘carpos’ of the Crustacea. A fully-developed medius exists in *Machilis* (Thysanura, Ectotropha), in the larvae of PHRYGANEIDAE (Trichoptera) and in those of the Coleoptera Adephaga. (Fig. 16.)

The fore tibiae are often specialized for cleaning purposes, and may bear combs which are used to polish the antennae.

Tarsi. The larvae of insects have no tarsi in the strict sense, but what we call a tarsus is really the empodium, see below.

While the femur, the medius and the tibia respectively represent the meros, carpos and propodos of the Crustacea, the tarsus of an insect is not a true segment, but is no more than a part of the propodos. In other words, the tibia and tarsus together come from the breaking up of a single primi-

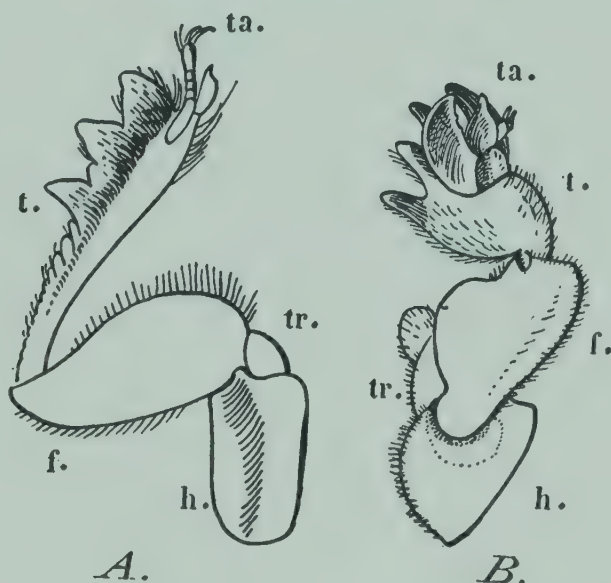
tive segment, the propodos. The proof lies in the fact that the tarsus has no musculature of its own.

The normal number of divisions of the tarsus (tarsal segments) may be five in certain groups of insects (Orthoptera, Coleoptera, Hymenoptera), and three in others (Palaeodictyoptera, Hemiptera), but these are reductions from the primitive number by the loss of some divisions.

The last division of the tarsus, which carries the claws, is known to systematists as the *onychium*. The claws of adult insects are modified processes of the tip of the propodos, having nothing in common with the claws of larvae, and emphatically not with the claws of Myriapoda or Arachnida.

Empodium. The final segment of the leg of an adult insect is a tiny nodule invaginated into the distal margin of the onychium, and upon which is inserted the tendon of the longitudinal flexor muscle, which arises from the femur, and passes through all the divisions of the tarsus without being attached to any of them (Fig. 17). The distal margin of the empodium bears either a sensory process, or sticky pads that assist in locomotion.

Fig. 18 – Fossorial legs: A, right fore-leg of *Canthon* (Coleoptera, Scarabeidae); B, left fore-leg of *Gryllotalpa* (Orthoptera); h, coxa; tr, trochanter; f, femur; t, tibia; ta, tarsus (after FOLSOM).



This segment has been given various names before its true identity was known (e.g. pulvillus, arolium, empodium). It was De Meijere who first showed that this was the terminal segment of the leg, the 'dactylos', which had been turned inwards. He called it the 'pretarsus', but we prefer to keep the old name of empodium.

In larvae the last segment of the leg is the empodium, which is then most often in the form of a claw, generally simple, but sometimes bifid. We also find, on the distal and tergal (dorsal) margin of the larval tibia two spines (present as a rule in Coleoptera), which we have named the 'epitarsal spines'. During pupation the larval claw (formed from the

dactylos) atrophies, and is withdrawn into the distal end of the tibia, while the two epitarsal spines extend over it, and take its place as a pair of claws. At the same time the tip of the larval tibia divides up to form the tarsal segments of the adult insect.

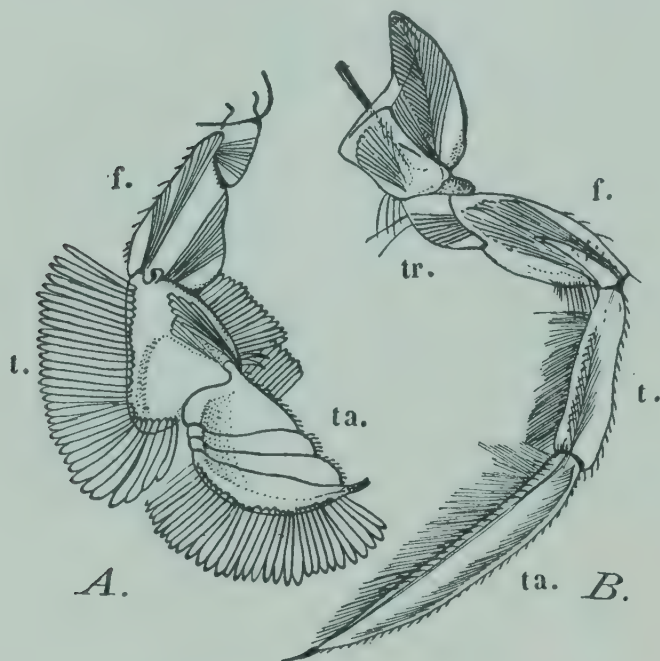


Fig. 19 – Swimming legs: A, right hind-leg of *Gyrinus* (Coleoptera); B, left hind-leg of *Corixa* (Heteroptera); tr, trochanter; f, femur; t, tibia; ta, tarsus (after WEBER).

Specializations of the Legs

Although generally adapted to locomotion on land, the legs are often modified for other purposes.

Many species live underground, and have fossorial legs, sometimes broadened into toothed shovel-like organs for digging out the soil (Fig.

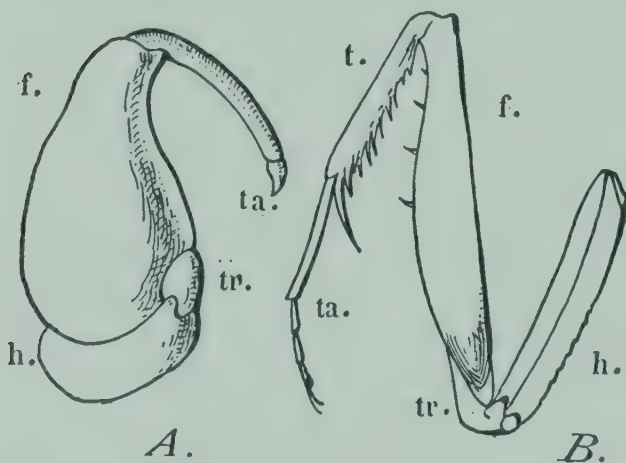


Fig. 20 – Raptorial legs: A, right fore-leg of *Pelocoris* (Heteroptera); B, left fore-leg of *Stagmomantis* (Dictyoptera; Mantidae); h, coxa; tr, trochanter; f, femur; t, tibia; ta, tarsus (after FOLSOM).

18), sometimes fringed with hairs for brushing aside the fine sand. There is a great variety of swimming modifications of the legs (Fig. 19). In many groups (MANTIDAE; Neuroptera; Hemiptera) the fore-legs have become

prehensile organs (Fig. 20); the pincers may be formed by bringing together the femur and the tibia (MANTIDAE; EMESINAE), or the tibia and the tarsus (HENICOCEPHALIDAE). We may mention also the hind-legs of PASSALIDAE (Coleoptera), which are greatly shortened, and function solely as stridulating organs, rubbing on the *pars stridens* of the coxae of the middle legs.

THE WINGS

Gegenbauer suggested that the wings of the pterygote insects were derived from thoracic gills, but the theory of Müller, deriving them from paranotal lobes, is now generally accepted.

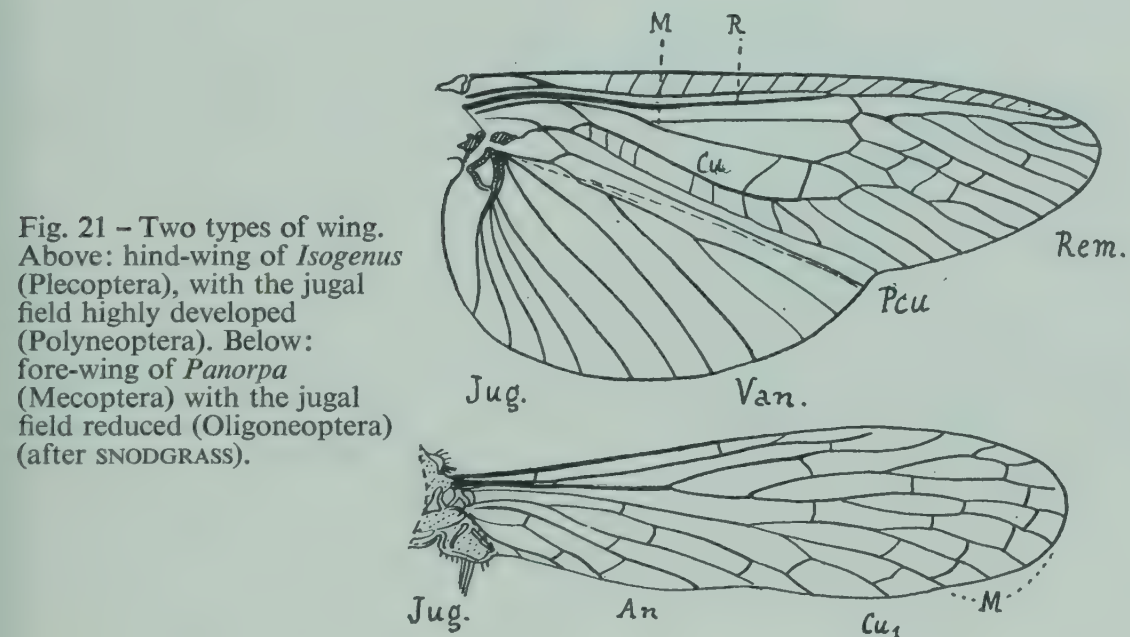


Fig. 21 – Two types of wing. Above: hind-wing of *Isogenus* (Plecoptera), with the jugal field highly developed (Polyneoptera). Below: fore-wing of *Panorpa* (Mecoptera) with the jugal field reduced (Oligoneoptera) (after SNODGRASS).

The membranous wing of an insect (Fig. 21) is more or less triangular, with an anterior margin (*costal*), a distal margin and a posterior margin (*vannal*). The anterior area of the wing, which is supported by longitudinal veins, was given the name *remigium* by Snodgrass; the posterior area, flexible, and capable of being folded, is the *van*, or *vannal field*, separated from the remigium by the *vannal fold*. The proximal part of the vannal margin of the wing is the *neala*, or *jugal field*, which in Neoptera has undergone secondary development to increase the lifting surface of the wing. The *squama* is a specialized part of the jugal field.

On the costal margin there is often to be seen an opaque, coloured patch known as the *pterostigma*.

The wing is hinged to the thorax through a series of sclerites; anteriorly comes the *tegula*, then the three axillary sclerites, or *pteralia*, of which the first two control the remigium and the posterior one the vannal field (Fig. 22).

Modification of the Wings

The wings have atrophied and disappeared in parasitic insects, in species living on high mountains, and in the females of certain species.

Among insects with fully developed wings, the fore-wings are often modified to act as covers for the hind-wings, and the latter developed more exclusively for flying. This evolution has taken place in several different lines of Neoptera, that is the groups in which the wings are folded backwards when at rest.

In Orthoptera the fore-wings are thicker than the hind-wings, and are called *tegmina*. The fore-wings of Heteroptera have only the basal half toughened, and are called *hemelytra*. Finally, Dermaptera and Coleoptera have true *elytra*, which take no part in flight, and which, moreover, are not affected when the hind-wings are reduced or lost in flightless forms.

In Strepsiptera the fore-wings are modified into balancers, organs of equilibrium; in Diptera and the males of COCCIDAE, on the other hand, it is the hind-wings that have been modified in this way, and which are then called *halteres*.

The higher pterygote insects have various methods of coupling the two pairs of wings together. In the beginning, among the most primitive forms, the two pairs must have been able to move independently, but their descendants have developed organs for locking together the two wings on each side. These organs arose by the adaptation of bristles (macrotrichiae) of the jugal margin of the fore-wing, and their interlocking with bristles arising from the costal margin of the hind-wing. A variety of mechanisms is found in Mecoptera and Lepidoptera.

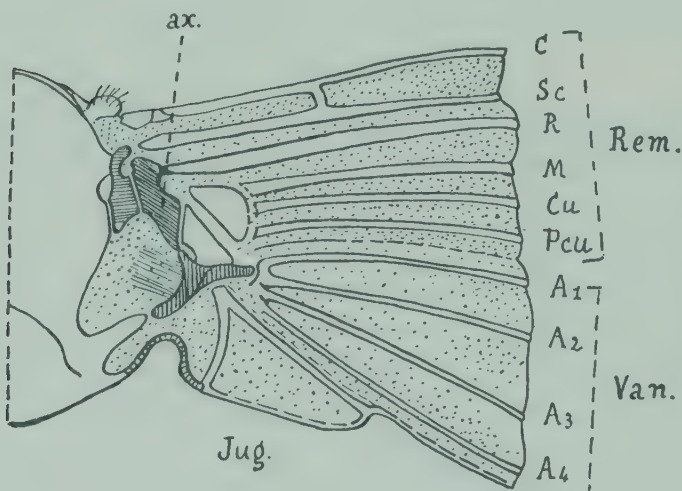


Fig. 22 - Base of the wing of an insect (diagrammatic). ax, axillary sclerites; Rem., remigium; Van., vannal field; Jug., jugal field (after SNODGRASS).

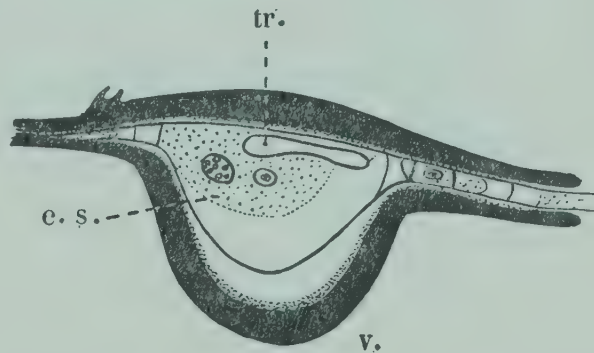
Structure of the Wing

The wings are large diverticula from the body-wall, with the two faces pressed together, and stretched over a series of thickened ribs, the *veins*. A wing-vein (Fig. 23) encloses a blood-space, which is an extension of the

general body cavity, and a trachea; sometimes also a nerve, if the wing bears sensory hairs or bristles, as in the elytra of Coleoptera Adephaga.

Comstock and Needham made a comparative study of the wings in adult insects and in pupae, in order to work out the relationships of the nerves. They showed that the tracheae of the wing were arranged in two groups, an anterior, or costo-radial group and a posterior, or cubito-anal group. This arrangement persists in the veins of the adult insect in Blattodea, Plecoptera and Homoptera, but in the majority of groups of insects there are modifications during and after pupation.

Fig. 23 – Cross-section of a wing-vein of *Notodonta* (Lepidoptera). tr, trachea; e.s., blood-space; v, ventral surface (after IMMS).



Wing venation. The arrangement of the wing-veins has assumed great importance in taxonomic work, and a variety of systems have been suggested for naming the veins, leading in the end to much confusion. The great merit of the work of Comstock and Needham is that it offers an almost universal system.

In the primitive insects, and generally in living Palaeoptera (Odonata, Ephemeroptera), and the Orthopteroid groups, the wings are folded longitudinally, so that some veins lie along a crest or ridge (convex veins) and some in a trough (concave veins). The distinctions between these two types of vein is less clear in the higher insects, but it is still possible to identify the various veins.

Fig. 24, after Comstock and Needham, with some modification in the jugal field, shows the hypothetical pattern of complete venation in a winged insect.

The *costa* (C) is simple and convex; the *subcosta* (Sc), concave, and rarely branched. The *radius* (R) divides into two branches, the radius proper (R_1) being convex, and reaching the distal margin of the wing, the *radial sector* (Rs) being concave, and forking into four (R_2 to R_5). The *medius* (M) has two branches: the anterior medius is convex and bifurcate (M_1 , M_2); the posterior medius is concave and divides into four (M_3 to M_6). The *cubitus* (Cu) also has two main branches, the anterior (Cu_1) being convex and bifurcate, the posterior concave and simple. Then come two *anal veins* which are convex, and which are succeeded by the jugal field, which in primitive Neoptera has a number of veins arranged in a broad fan.

This plan has undergone a number of evolutionary changes. Thus the complete *medius* exists only in insects of the Palaeozoic, and in Ephemeroptera alone among living insects. Most insects have lost the anterior branch of the medius, so that what we call the medius in practice is a concave vein. A whole series of modifications of the general plan have come about by the suppression of certain veins, deflection of existing ones, and even by the appearance of supplementary veins.

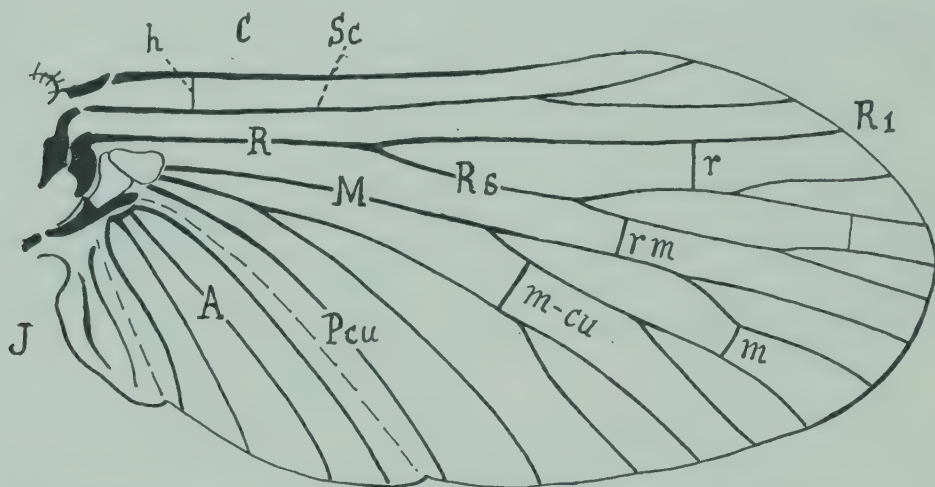


Fig. 24 - Venation of the wings (diagrammatic) (after COMSTOCK and NEEDHAM).

There are not only longitudinal veins in the wing, but cross-veins as well. In the Palaeodictyoptera of the Palaeozoic period the wing-membrane was entirely covered with a network of small veins, the *archedictyon* (Fig. 25), which has gradually disappeared in later insects, leaving only a few traces. The cross-veins that occur in the wings of living insects are supposed to be remnants of the archedictyon, but there is no certain proof of this.

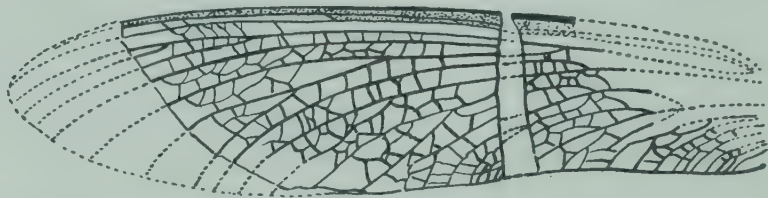


Fig. 25 - Fossil imprint of the wing of *Mecynoptera* (Palaeodictyoptera) of the Carboniferous, showing the archedictyon (after HANDLIRSCH).

However that may be, the cross-veins most usually present are as follows: *humeral cross-vein* (h), between C and Sc; *radial cross-vein* (r) between R₃ and R₄; *radio-median* (r-m) between R and M; *median cross-vein* (m) between M₂ and M₃; and *medio-cubital* (m-cu) between M and Cu.

The cross-veins mark out the cells, the names of which are based upon the names of the veins, according to Comstock and Needham's

system. Cells are of two categories, basal and distal, in relation to the cross-veins. Thus the median cross-vein separates the median basal cell, which is *closed*, from the median distal cell, which is *open*, that is to say, it reaches to the margin of the wing.

THE ABDOMEN

The **number of segments**. The abdomen of insects is divided into segments, which differ from those of the thorax in not possessing legs, other than rudimentary ones in the lower groups. Since the abdominal segments have no legs, they also have no pleural sclerites, since these, as we have seen, are derived from the basal segment of the leg, the subcoxa.

The number of abdominal segments, or *urites*, is restricted to six in Collembola, but in other insects the complete number is twelve. Study of the embryonic development of Collembola shows that no more than six segments are present from the earliest stages, and consequently the adult number has not been arrived at by reduction. The Collembola have preserved this limited number of abdominal segments from their earliest

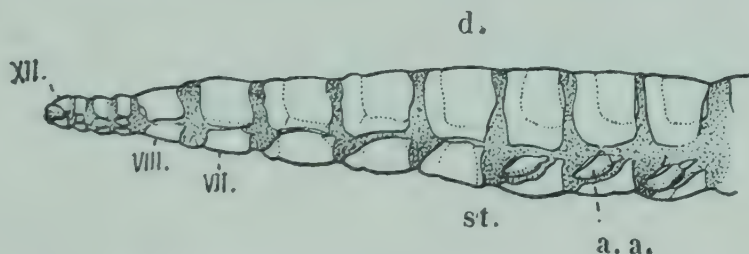


Fig. 26 – Abdomen of *Eosentomon* (Protura), in the adult state, showing twelve abdominal segments: a.a., abdominal appendages of the first three segments; d., dorsal surface; st., sternal surface (after WEBER).

ancestors (the *protomorphous* type). It may also be assumed that the ventral tube, retinaculum and furca of the Collembola, are vestiges of abdominal legs, transformed into jumping organs. See Pl. 1, IV (2) (page 89).

The Myriapoda have few segments at the beginning of their larval life, but these increase in number at each moult, by budding from the penultimate segment (*anamorphous* type). The Protura (Fig. 26), which have 12 abdominal segments in the adult, like other insects, only arrive at this number gradually during successive larval instars, and so show an *anamorphosis* like that of the Myriapoda.

In all the other insects, Thysanura and Pterygota, the maximum of twelve abdominal segments is settled at the beginning of embryonic development (*epimorphous* type), but during development this number may be reduced, by loss or invagination of the posterior segments, accompanied sometimes by loss of the anterior sternites, or their fusion with the metathorax. It follows, then, that the number of visible segments in adult insects is very variable.

The anus and genital orifice. (Figs. 27, 28, 29.) The anus is terminal, and so it is primitively situated on the twelfth segment. The genital orifice is ventral: in the males it opens immediately behind the ninth sternite, and in the females between the eighth and ninth sternites, or on the hind margin of the ninth sternite. The venter of the abdomen may thus be divided into three regions in relation to the genital orifice.

All the visible segments before the eighth constitute the *pregenital* region (visceral). The eighth and ninth sternites, which adjoin the genital orifice, and some parts of which contribute to the genital armature, are the *genital region*. Finally, there is a *postgenital region*, after the ninth sternite, and the last few urites which enter into it are often very much reduced sclerites surrounding the anus; the postgenital region is often called the *proctiger*.

Appendages of the abdomen. Although the abdominal segments of insects never bear true legs, all three of the regions that we have just defined often have appendages for other purposes.

The jumping apparatus of the Collembola, as we have seen earlier, is made up of the modified appendages of the first, third and fifth segments. In the Protura, the vestiges of abdominal legs can be traced on the first

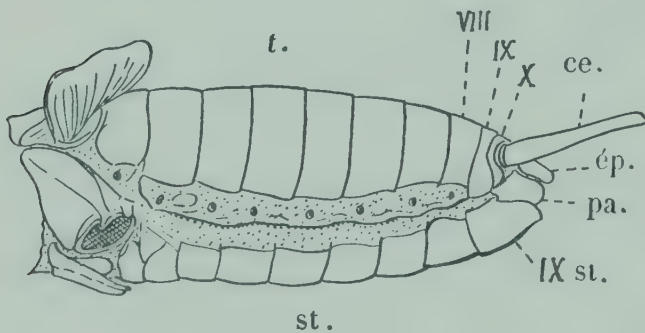


Fig. 27 – Abdomen of *Gryllus* (Orthoptera), in lateral view: st, sternites; t, tergites; pa, paraproct; ép, epiproct; ce, cercus (after SNODGRASS).

three segments, and in the Thysanura the first seven segments, the entire pregenital region, has a pair of ‘styles’ on each segment, the nature and homologies of which are very controversial. In the aquatic larvae of Ephemeroptera, Plecoptera and Megaloptera these same seven segments have paired tracheal gills, which in Megaloptera are even articulated.

The genital region has its appendages, which are called *gonopods*.

In males of many groups the genital armature, or copulatory organ includes a pair of appendages belonging to the ninth sternite, which are called ‘styles’ in Thysanura, Ephemeroptera and Blattoidea, ‘harpagonia’ in Hemiptera, Mecoptera and Trichoptera, and ‘harpes’ in Lepidoptera. They are absent in Coleoptera and Hymenoptera.

In females the genital armature includes appendages of both the eighth and the ninth segments, and is especially highly developed in those insects that are provided with an *ovipositor* (Fig. 28) for the purpose of laying eggs.

The ovipositor of a grasshopper consists of one pair of anterior ventral valves belonging to the eighth sternite, a pair of posterior ventral valves belonging to the ninth sternite, and pair of lateral valves arising from the side-piece (coxite) of the ninth segment. The six valves are known collectively as the *gonapophyses*.

Among Hymenoptera, female sawflies have an ovipositor constructed like that of the Orthoptera, but the Aculeata (bees and wasps) use this apparatus as a sting, and the component parts are then referred to as stylets.

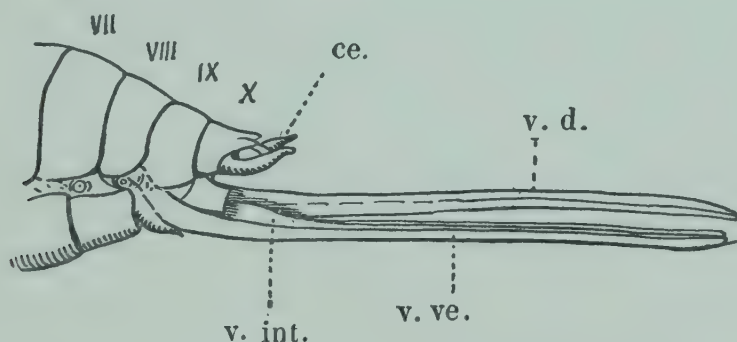
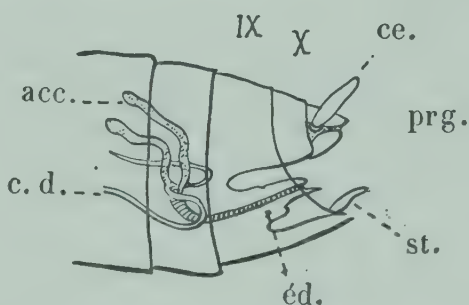


Fig. 28 – Ovipositor of *Conocephalus* (Orthoptera): ce, cercus; v.ve., anterior ventral valve (8th sternite); v.int., posterior or internal ventral valve (9th sternite); v.d., dorsal or lateral valve (coxite of 9th urite) (after IMMS).

Finally, there is a pair of appendages belonging to the postgenital region, known as the *cerci* (Fig. 27). In embryo the cerci are seen to be the appendages belonging to the eleventh segment, but the atrophy of the eleventh segment itself has left the cerci apparently attached to the tenth segment in primitive insects, notably in Thysanura, Ephemeroptera and Blattoidea. Similar appendages appear to arise from the ninth segment in beetle larvae, but this apparent position is secondary, as a result of the

Fig. 29 – Posterior segments of the abdomen of a male insect (diagrammatic): prg., proctiger; ce, cercus; st, style; ed, aedeagus; c.d., vas deferens; acc., accessory glands of the genitalia (after SNODGRASS).



atrophy of both the tenth and the eleventh segments; these cerci may be called *urogomphae*.

It only remains to mention the false legs which are present ventrally on the abdomen of many larvae, particularly of Lepidoptera, Hymenoptera and Mecoptera, and which have no significance as true segmental appendages. A common modification is that in which the proctiger becomes an

unpaired tube as an aid to locomotion, and in that case it is known as a *uropod*, or *pygopod*.

Male copulatory apparatus. The actual copulatory, or intromittent organ is the *aedeagus* (Fig. 29), which is produced by sclerotization of the intersegmental membrane surrounding the genital orifice, and is therefore a secondary development. The genital armature which surrounds the aedeagus is built up from the segmental appendages of the ninth sternite, and other parts of the same segment.

The aedeagus arises by a prolapsus of the genital duct, the external, reflexed part being sclerotized, and more or less tubular, surrounding an inner, membranous part called the *internal sac*. This outer sclerotized trumpet is divided into two parts, basal and distal, which can be more or less telescoped. The basal organ (phallobase) often bears lateral sensory lobes (parameres), and the distal organ forms an inner lobe, or *penis*. These structures are extraordinarily variable throughout the insects, and specialists in different groups have given them a variety of special names. There is need for a revised nomenclature of genitalia which would show the true homologies in all groups.

3

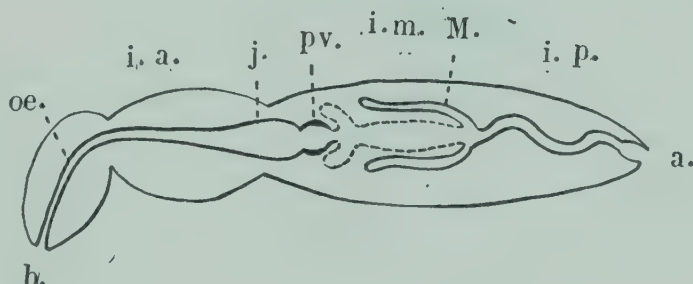
Internal Anatomy

THE DIGESTIVE SYSTEM

The alimentary canal varies in length in insects of different groups. In Thysanura, and in the larvae of Hymenoptera, Lepidoptera and Diptera Nematocera it is a simple tube, and almost straight, but in other insects it is longer, and coiled, reaching a high level of complication in Homoptera and in the larvae of Diptera Cyclorrhapha. As a general rule, the alimentary canal is short in carnivorous insects and long in phytophagous ones.

Morphologically, the canal is derived from two different sources (Fig. 30). The fore-gut (stomodeum) and hind-gut (proctodeum) are invaginations of the integument, and are ectodermal; the mid-gut (mesenteron) arises as an endodermal sac, the ends of which attach themselves to the stomodeum and proctodeum respectively.

Fig. 30 – Diagram of the alimentary canal of an insect:
i.a. and i.p., fore-gut and hind-gut (continuous line); i.m., mid-gut (dotted line); b, mouth; oe, oesophagus; j, crop; pv, proventriculus; M., Malpighan tubules; a, anus (after IMMS).



The Fore-gut. The lining of the fore-gut is a cellular layer continuous with the hypoderm of the cuticle, and covered, like the cuticle, with chitin. Surrounding this on its outside is a layer of longitudinal muscles, followed by a layer of circular muscle. The final outer covering is the peritoneal membrane.

The mouth leads straight into the *pharynx*, which is most highly developed in sucking insects, where it has a powerful muscular pump. Often salivary glands open into the pharynx. After the pharynx comes the *oesophagus* (Fig. 31 *oe*), extending from the head into the prothorax, and leading into the *crop*, a dilation of the alimentary canal that is often very big. In *Dytiscus* the crop is a large folded sac, which can be distended, and in Diptera it is a long lateral diverticulum, in which food can be accumulated, and impregnated with salivary juice.

The *proventriculus*, or gizzard (Fig. 31 *pv*) follows after the crop, and is most prominent in insects that have chewing mouthparts. The lining of the proventriculus is raised up into ridges, which are chitinized at the crest, and equipped with filtering hairs at their base. Strong muscles move the ridges, and bring about a thorough mixing of the food, which is held

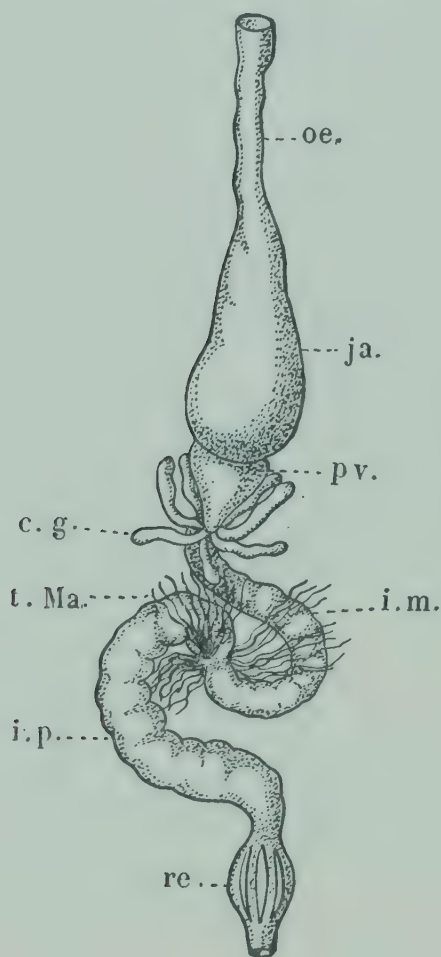


Fig. 31 – Alimentary canal of *Periplaneta americana* (Dictyoptera): oe, oesophagus; ja, crop; pv, proventriculus; c.g., gastric caeca i.m., mid-gut; t. Ma., Malpighian tubules, very numerous; i.p., hind-gut; re, rectum, with rectal glands (after BORDAS).

trapped in the proventriculus by the *cardiac valve*, separating it from the mid-gut (Fig. 32).

Mid-gut. The mid-gut begins at the cardiac valve, and extends as far as the openings of the *Malpighian tubules*. It occupies the endodermal part of the alimentary canal: its epithelium is not chitinized, and the surrounding muscles are in the reverse order to those of the fore-gut, with the circular muscles next to the epithelium, and the longitudinal muscles outside these. All the muscles are striated.

The anterior part of the mid-gut is often dilated into a *chyliferous vesicle*, the surface of which is increased in area by a variable number of enteric caeca, or side-tubes (Fig. 31 *c.g.*). These sometimes house symbiotic bacteria which assist in the digestion of some part of the food.

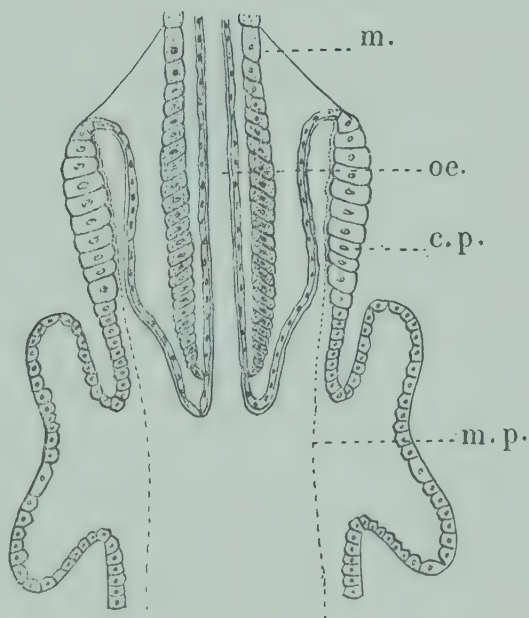
When the food passes into the mid-gut it is wrapped in a chitinous

membrane, called the *peritrophic membrane* (Fig. 32), which is secreted by special cells in the cardiac valve. The cells of the epithelium of the mid-gut, some of which secrete digestive fluids, and others of which absorb nutriment from the food, are able to function because the peritrophic membrane is permeable. Afterwards the waste products of digestion, still enclosed in the peritrophic membrane, pass into the hind-gut ready to be excreted. The end of the mid-gut is closed by a *pyloric sphincter*.

Hind-gut. Here, again, is the same ectodermal structure as in the fore-gut. The beginning of the hind-gut is indicated by the openings of the Malpighian tubules (Fig. 31 *t.Ma.*), which are also ectodermal in origin, and of which we shall have more to say later on.

Generally the hind-gut is in three parts: the *small intestine*, the *large intestine* and the *rectum*. The small intestine is often very elongate; the large intestine sometimes has diverticula containing symbionts; and the rectum is more or less dilated, pear-shaped, and bearing on its lining papillae, or *rectal glands* (Fig. 31 *re*), of which the function is obscure. Close to the anus there open the *anal glands*, which are always well developed in Coleoptera, and which in certain genera (e.g. *Brachinus Paussus*) can produce an explosive and offensive fluid.

Fig. 32 – Section of the cardiac valve of a larva of the Diptera Nematocera: oe, oesophagus; m, muscular covering of the oesophagus; c.p., cells which generate the peritrophic membrane; m.p., peritrophic membrane (after IMMS).



THE RESPIRATORY SYSTEM

The great majority of insects breathe by means of a tracheal system, in which ectodermal invaginations branch into all parts of the body, and open to the exterior by *spiracles*, disposed in pairs on the segments of the thorax and abdomen (Fig. 33). Aquatic larvae and nymphs of many kinds obtain the oxygen they need for respiration by means of *tracheal gills*, which are evaginations or extensions outwards of the body-wall. Along with tracheal gills, normal spiracles may also be present, but there are

insects without tracheal gills, and with the normal spiracles completely closed. In these insects respiration is cutaneous.

Spiracles. The spiracles open laterally on the pleural parts of the intersegmental membranes, just anteriorly to the margin of the segment to which they belong.

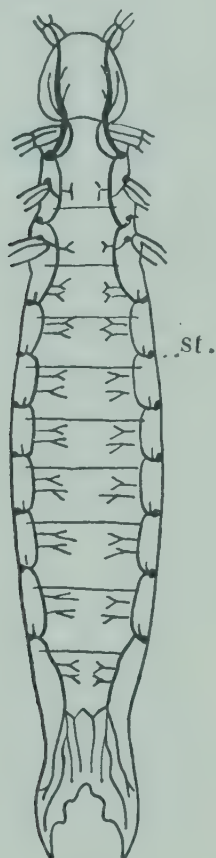


Fig. 33 – Tracheal system of *Japyx* (Thysanura): st, stigma (spiracle) (after IMMS).

The number of spiracles is variable. In embryonic insects 12 pairs can be counted, 3 thoracic and 9 abdominal. The maximum number observed in any adult insect is 11 pairs, in *Japyx* (Thysanura) (Fig. 33), but this is made up of 4 thoracic pairs (two pairs on the metathorax) and 7 abdominal ones on the seven visceral (pregenital) segments (see above). In the great majority of adult insects there are no prothoracic spiracles, and typically there are 2 pairs of thoracic ones and 8 pairs of abdominal ones, making 10 pairs in all. Nevertheless, there are frequent deviations from this number.

Larvae with the complete set of ten pairs of spiracles are called the *holopneustic* type. Often the metathoracic or the first abdominal pair is missing, giving the *peripneustic* type. When only the last pair of abdominal spiracles remains open we have the *metapneustic* type, as in dipterous larvae, and when all the spiracles are closed the type is called *apneustic*.

A typical spiracle consists of an annular sclerite, or *peritreme*, which is fitted with some kind of closing mechanism, and which opens into an inner chamber, or *atrium*, from which the tracheae lead off. The entrance of the

atrium is protected by a sieve of hairs, and by glandular secretions. The shape and detailed structure of the spiracles, however, varies greatly in different groups of insects.

The simplest kind are merely circular or oval apertures, which can be closed by the peritreme, either by means of two lips which come together and move apart, or by a fringe of cilia which filters the air (e.g. in *Lepidoptera*). But in a great many larvae that live in the ground, or in the interior tissues of plants, the spiracles are closed, and air reaches the atrium by diffusion through the cuticle, which is specially thin at this point.

The spiracles of *SCARABAEIDAE* (Fig. 34 C) look like small horse-shoes surrounding the atrium, which has no opening to the exterior. Instead, the horse-shoe-like plate has a large number of spots where the cuticle is thin, and air diffuses through these into a dilation of the atrium.

The 'double' spiracles of certain beetles (Fig. 34 A) also have the atrium completely sealed off, but it is prolonged beneath the integument as two chambers, which may be simple or convoluted (*CURCULIONIDAE*). This gives the appearance of a double spiracle, though in fact there is no opening to the exterior at all. The eighth pair of spiracles in the aquatic larvae of the beetle *Donacia* is of this type, but further elaborated by being drawn out into a long, sharp-pointed spur, which is used to pierce the aerated vessels of submerged plants. The two chambers of the atrium run along this spur, and open by means of a number of ciliated slits, through which air is drawn out of the plant.

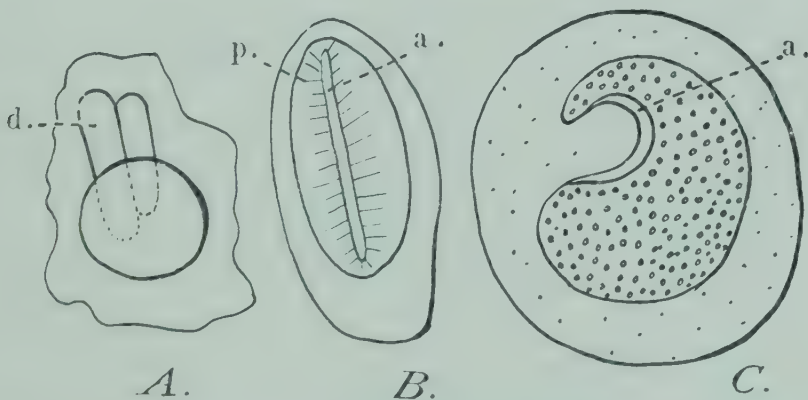


Fig. 34 - Three types of spiracle in the larvae of Coleoptera: A, bifid type in *Curculionidae*; B, simple, two-lipped type in *Lymexylidae*; C, cribriform type in *Lucanidae*. a, aperture of atrium; p, peritreme; d, diverticula of the atrial chamber (after PAULIAN).

Tracheae. These are tubes which are kept from collapsing by an elastic spiral filament which runs in the endocuticle (*taenidium*). The main tracheal trunks arise from the atrial chambers of the spiracles, and are joined together by longitudinal tracheae; these in their turn are linked by

transverse branches. The longitudinal tracheae are arranged in two systems: a ventral one serves the ganglia of the nerve-chain, and the sternal muscles; and a more important dorsal one, which ramifies into tracheoles within the head, the appendages, the wings and the tergal musculature.

In many winged insects the tracheae have certain big dilations which are membranous, and without the spiral stiffening. Such *air-sacs* are highly developed in the pterothorax and the abdomen of bees and flies. Fig. 35.

Gills in insects. Aquatic larvae have gills of two kinds, tracheal gills and blood-gills.

Tracheal gills are tubular or flattened diverticula, supplied with tracheae. They are by far the most common type, and are found on the abdominal segments of the larvae of Ephemeroptera, Megaloptera, and many beetles. The larvae of Anisoptera (Odonata) have tracheal gills in the rectum, and the larvae of Zygoptera have them as broad perianal lobes.

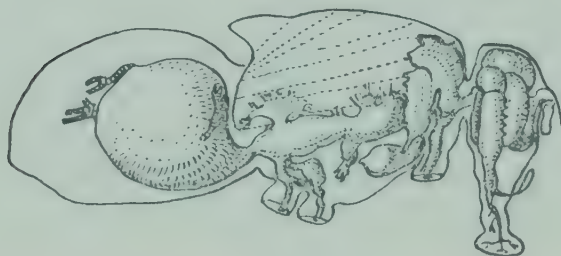


Fig. 35 – Longitudinal section of a fly (*Musca domestica*), showing the air-sacs (after BERLESE).

Blood-gills are found in Trichoptera and some Diptera, in particular in the larvae of CHIRONOMIDAE. Here we have finger-like tubes which can be everted, and which are without tracheae, but full of blood.

Respiration. It was thought for a long time that the air-sacs of insects functioned as lungs, and that an exchange of oxygen took place there, as well as in tracheal gills. This is not so; there is no respiratory action in the sacs or in the gills, which, like the tracheae themselves, merely conduct the air to the tissues of the body. The body takes up its oxygen solely by means of special cells which cluster round the tracheoles in certain organs. The insect maintains a circulation of air in its tracheae by movements of the abdomen, and some spiracles function during the intake of air (*inspiration*) while the others function during the expulsion of air (*expiration*). There is no general rule about which spiracles perform which function.

THE CIRCULATORY SYSTEM

In the insects the blood is not carried in blood-vessels, but fills the general cavity of the body and of the appendages. The space occupied by

the blood is called the *haemocoele*. The circulation of the blood is really a stirring, brought about by a dorsal organ called the heart; this is a tube, open posteriorly and with a series of paired lateral openings called ostioles, while anteriorly it continues as an aorta, which divides into branches as it passes into the head.

Haemocoele. The haemocoele of the body of the insect is divided into three chambers, or *sinuses*, by means of *diaphragms*, partitions of fibrous muscle running horizontally. The dorsal chamber, the *pericardial sinus*, surrounds the heart; the middle one, the *visceral sinus*, surrounds the alimentary canal; and the ventral, or *perineural sinus*, surrounds the ventral nerve-chain.

The dorsal vessel. The dorsal vessel, or heart, consists of a series of chambers, each of which communicates with the haemocoele by means of a pair of ostioles. The chambers are separated from each other by valves which direct the flow of blood in the heart from behind forwards, towards the aorta. Primitively there must have been one chamber to each of the thoracic and abdominal segments, but in nearly all living insects the number of chambers is reduced, and in higher groups there are often only eight, all in the abdomen.

Often in winged insects there are accessory pulsatory organs, either in the thorax or in the head.

The blood is generally colourless, but may contain toxic substances. For example, in Meloid beetles the blood contains one quarter to one half per cent of cantharidin, a very violent irritant poison. Those beetles which have toxic substances in their blood sometimes show the phenomenon known as *reflex bleeding*, by which they are able to exude droplets of blood from their joints as a means of defence.

EXCRETORY ORGANS

The most important of these are the Malpighian tubules, but there are other organs of secondary importance, the pericardial cells (dorsal nephrocytes), the oenocytes, and the fatbody.

Malpighian tubules. As we have seen above, these are long tubules which open into the hind-gut close to its origin, and are similarly of ectodermal origin. They are variable in number. The Palaeoptera and the Polyneoptera may have a great number (Fig. 31), as many as 120 (*Polynephridia*). In the Oligoneoptera and the Paraneoptera the number is reduced to 6 or 4 (*Oligonephridia*). They always occur in pairs.

The Malpighian tubules of Oligonephridia are specialized, and often consist of different pairs. Sometimes the two free ends of a pair are united to form a long loop (the *looped type*). In those beetles with six pairs of tubules the distal ends of the tubules often pass beneath the muscular

sheath of the large intestine, and extend below it (the *cryptonephridial type*, Fig. 36 C).

The histology of Malpighian tubules varies greatly, indicating that they have a variety of different secretory functions, but it is undisputed that their principal function is to extract and eliminate waste products from the blood.

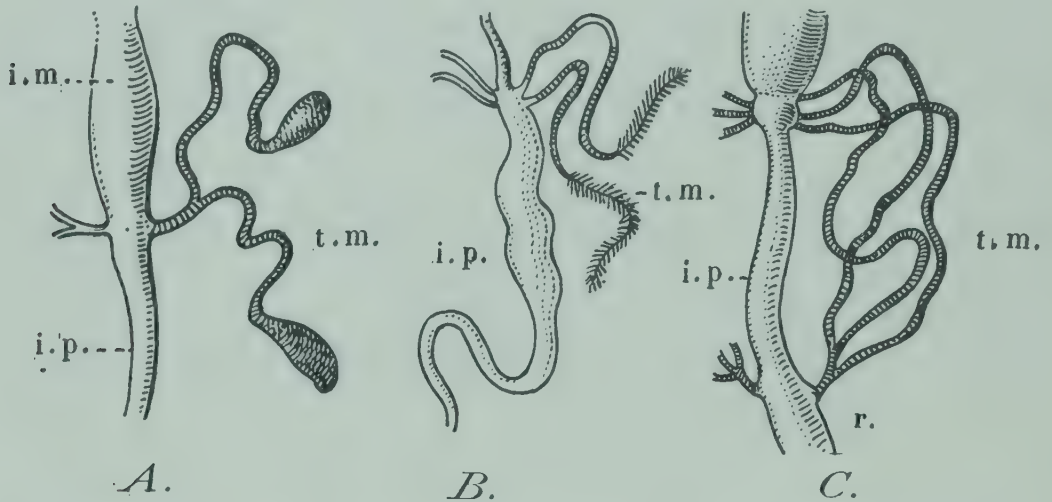


Fig. 36 - Three types of Malpighian tubule: A, *Phora pallipes* (Diptera); B, *Melolontha vulgaris* (Coleoptera); C, *Oedemera dispar* (Coleoptera). i.m., mid-gut; i.p., hind-gut; t.m., Malpighian tubule. In the cryptonephridial type shown in fig. C, the tubules are attached to the rectal wall (r) by their distal ends.

Pericardial cells. A variety of cells is present in the plasma of the blood: haemocytes, amoebocytes, phagocytes. The last of these are especially numerous on the pericardial wall, and form masses extending along the dorsal vessel. These pericardial cells, or *nephrocytes*, constitute a sort of makeshift kidney, ridding the blood of its toxins at the same time that they function as phagocytes.

Oenocytes. This name is given to certain groups of cells that are distributed in the pleural parts of each abdominal segment, and which are believed to arise during the embryonic development of the spiracles, hence to be of ectodermal origin. These cell-groups are provided with tracheoles, and the cells are wine-coloured, with a big nucleus. The exact function of the oenocytes is still in dispute, but doubtless they are analogous to the pericardial cells.

Fatbody. The fatbody consists of irregular groups of polygonal cells containing many intracellular spaces or *vacuoles*. The vacuoles may enclose a number of intrusive substances, but especially globules of fat. The fatbody is derived from the mesoderm.

In many insects the fatbody lies in two layers, a visceral one round the alimentary canal, and a parietal one beneath the integument (Fig. 37). The histological structure of the cells changes during the life of the

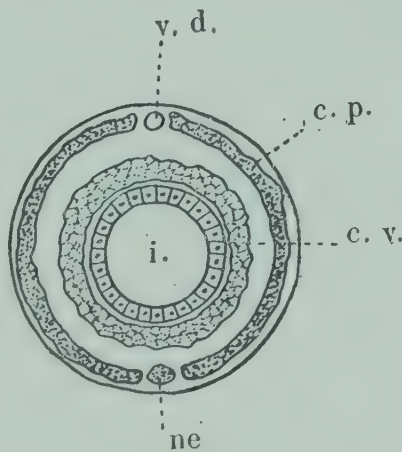
insect: the nuclei are rounded in the young insect, but become star-shaped as the insect ages.

Fatbody has a double function, firstly to extract waste products from the blood and store them as urates, and secondly to constitute a reserve store. According to Berlese, the products of excretion accumulate in the parietal fatbody, while the visceral fatbody is principally a reserve store for use during the reproductive period. The fact is that the fatbody plays a great part in excretion, and in holometabolous insects the urates accumulated in the fatbody during larval life are discarded through the intestine after metamorphosis.

Luminous organs. In certain beetles (Lampyridae, Elateridae) the parietal fatbody has been converted into luminous organs. A layer of granular cells, richly supplied with nerves and with tracheoles, is situated in the cuticle, and beneath it is a reflecting layer made up of cells packed with crystals of urates and xanthine. Light is produced by chemical reaction: a greasy substance (*luciferin*) oxidizes in the presence of an enzyme (*luciferase*) and gives an oxyluciferin, which is luminescent. The speed of this reaction can be controlled by the insect.

The light produced by glow-worms (LAMPYRIDAE) or fire-flies (ELATERIDAE) is a cold light, with a very restricted spectrum, and with a luminous efficiency far greater than any source of light invented by mankind. The LAMPYRIDAE produce this light at all stages of the insect, after leaving the egg. The colour of the light varies in different species, from greenish to red.

Fig. 37 – Diagrammatic cross-section of the larva of an insect: i, intestine; v.d., dorsal vessel; ne, ventral nerve-chain; c.p., parietal layer of fat-body; c.v., visceral layer.



THE NERVOUS SYSTEM

The nervous system is composed of three parts, a central nervous system, or ganglionic chain, a visceral system and a peripheral system.

Central nervous system. The central nervous system consists of a double chain of ganglia, joined together by connective branches. At the head of the chain is the *supra-oesophageal ganglion*, or 'brain', with two connective nerves encircling the oesophagus (*peri-oesophageal collar*) and

meeting in the *sub-oesophageal ganglion*. From this there leads posteriorly a ganglionic chain, attached to the ventral wall of the body-cavity, and made up of three pairs of thoracic ganglia, and a series of abdominal ones, of which the posterior ganglia are always more or less fused together (Fig. 38).

The nerve fibres that run transversely between the two ganglia of each pair are the *commissures*; those uniting successive ganglia are called *connectives*. Very often the thoracic ganglia on the one hand, and

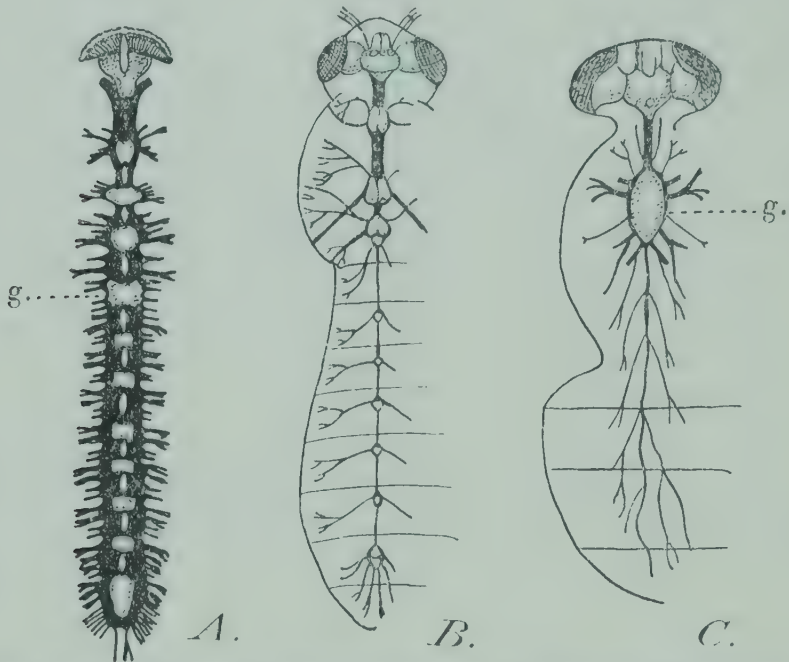


Fig. 38 - Three types of nervous system: A, *Machilis* (Thysanura); B, *Chironomus* (Diptera); C, *Musca* (Diptera). g, ganglion (after IMMS).

the abdominal ones on the other fuse together into *ganglionic centres*. The ganglia are surrounded by an epineural membrane, under which are the ganglionic cells: these are generally unipolar, and are embedded in a kind of neuroglia which encloses the longitudinal fibres of the nerve cells.

The brain. The brain, or supra-oesophageal ganglion (Fig. 39) is in three parts: *protocerebrum*, a fusion of very many optical ganglia; *deutocerebrum*, or olfactory lobe, with the antennary nerves; and the *tritocerebrum* from which arise the perioesophageal connectives. These three regions of the brain correspond with three primitive somites of the head, anterior to the mouth: the ocular, antennary and postantennary somites.

Similarly, the sub-oesophageal ganglion seems to have arisen by the fusion of the three post-oral ganglia, since it gives rise to the mandibular, maxillary and labial nerves.

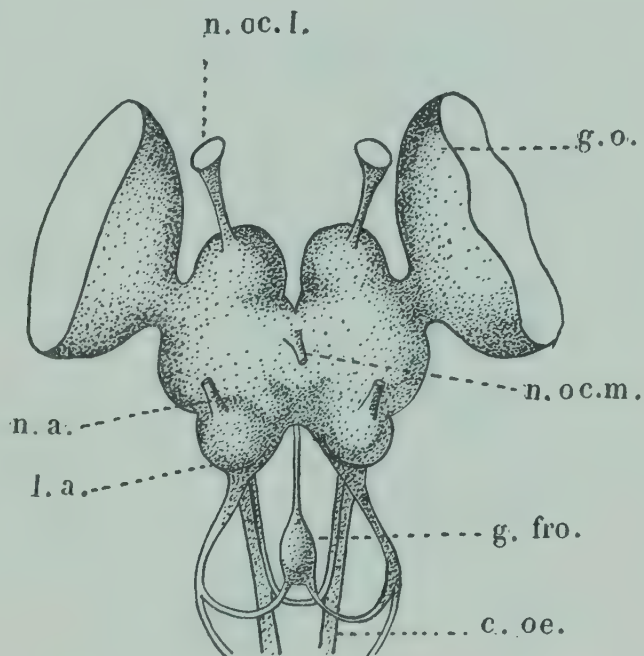
Visceral nerve-system. Firstly, there is a *dorsal sympathetic*, or *stomato-gastric* system, composed of the ganglia and nerves that are situated on the

dorsal surface of the oesophagus and fore-gut, and innervating successively the alimentary canal, the dorsal blood-vessel, and the pericardial organs. In addition there is also a *ventral sympathetic* system made up of transverse nerves associated with the ganglia of the abdominal chain.

Peripheral nerve-system. This is built up from a network of fine fibres, and of multipolar nerve cells, situated beneath the hypoderm. Certain of these fibres are associated with the bipolar cells that occur at the bases of the setae and sensillae with which the integument is covered. This peripheral system is entirely sensory.

Corpora allata. To the oesophageal ganglia are attached the *corpora allata*, ganglionic masses that are not nervous in origin, but are found closely applied to the dorsal and external surface of the fore-gut. These bodies, which are of ectodermal origin, are innervated only from the stomato-gastric system, and seem clearly to be organs of internal secretion (endocrine organs). It is now known that they secrete hormones that retard metamorphosis.

Fig. 39 – Brain of *Caloptenus* (Orthoptera): g.o., optic nerve and ganglion; n.oc.l., nerve to the lateral ocellus; n.oc.m., nerve to the median ocellus; l.a., antennary lobe; n.a., antennary nerve; g.fro., frontal ganglion; c.oe., perioesophageal commissure (after BURGESS).



THE SENSE-ORGANS

Organs of touch. All over the integument are found hairs which have nerve-cells at their base, and smaller organs, scarcely protruding above the surface of the cuticle, which are called *sensillae*. These latter are diverse in form—cones, papillae, plates—and are always connected with the peripheral nervous system. Their function is apparently tactile.

Organs of smell and taste. The epipharynx and the hypopharynx have similar organs, which are used as gustatory, or taste-organs. On the other hand, the organs of smell seem to be concentrated in the antennae or the palpi, either as individual sensillae dispersed over the surface, or as

aggregations of sensillae built up into a distinctive organ. Most of the time these latter take the form of vesicles (Fig. 40) open to the exterior, and inside which the receptor ends of the nerve-cells protrude.

Organs of sight. Many insects live underground and have no eyes. Instead, they are sensitive to the general illumination, and their response has been shown experimentally.

The eyes of larvae are *stemmata*, or lateral ocelli (Fig. 41). These consist of a hyaline ectodermal part (*cornea*), and a retinal part of pigmented neuro-epithelial cells, the termination of the ocellary nerve.

The *median ocelli* of the lower insects (Fig. 42) have much the same structure as *stemmata*. In the neuro-epithelial layer they develop pigmented cells and rhabdomes, round which cluster the retinal cells.

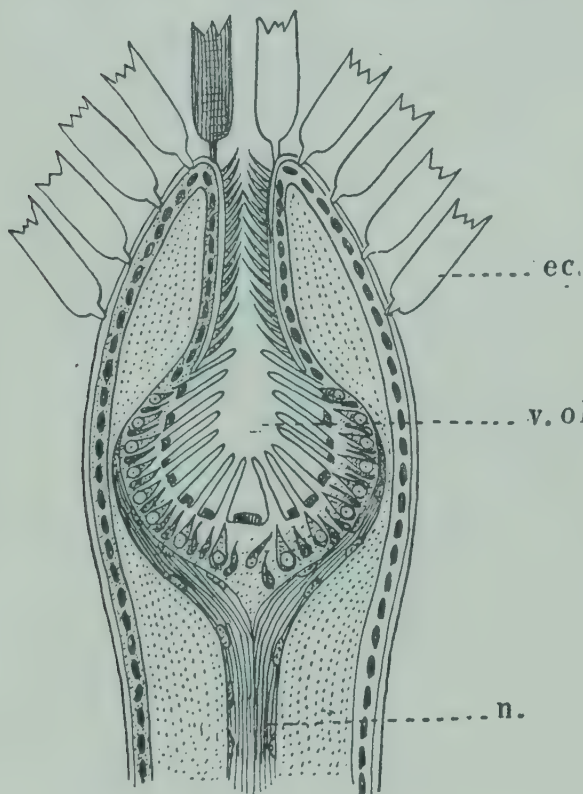


Fig. 40 – Tip of the labial palp of *Pieris* (Lepidoptera): v.ol., olfactory vesicle; n, olfactory nerve; ec, scales (after IMMS).

Compound eyes (Fig. 43) are aggregations of simple eyes, or *ommatidia*, arranged beneath a corneal layer which is divided into facets, one for each ommatidium. The bases of the ommatidia rest on a basal membrane that is perforated so that the nerves and tracheoles can pass through it. The complete eye is linked with the protocerebrum by a thick and complex optic nerve, in which the fibres pass through two successive chiasmata.

There are a variety of ommatidia. In the *eucone* eye (Fig. 44), the four crystalline cells secrete a true crystalline cone, which is intracellular, and highly refractive. This is the commonest type of compound eye. The *pseudocone* eye of many Diptera has a semiliquid cone. The *acone* eye has

Fig. 41 - Ocellus of a larva of *Dytiscus*: cu, cuticle; re, retinal cells; vi, hyaline cells (after IMMS).

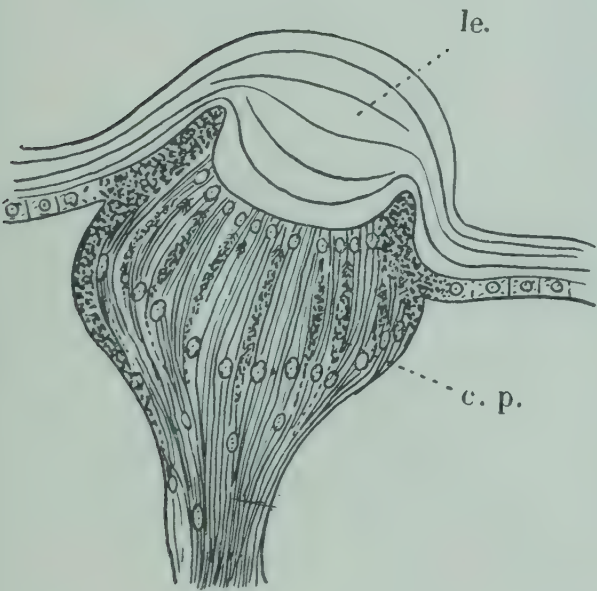
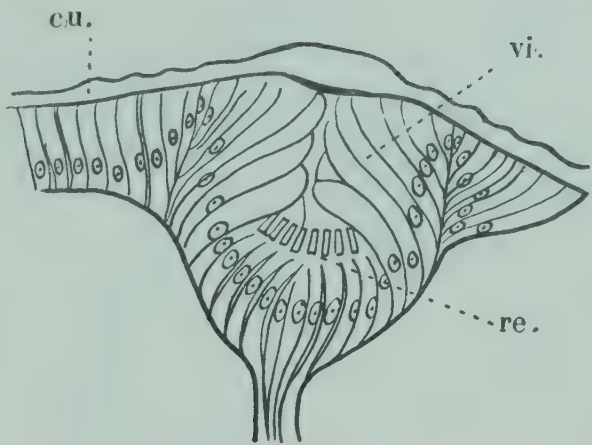
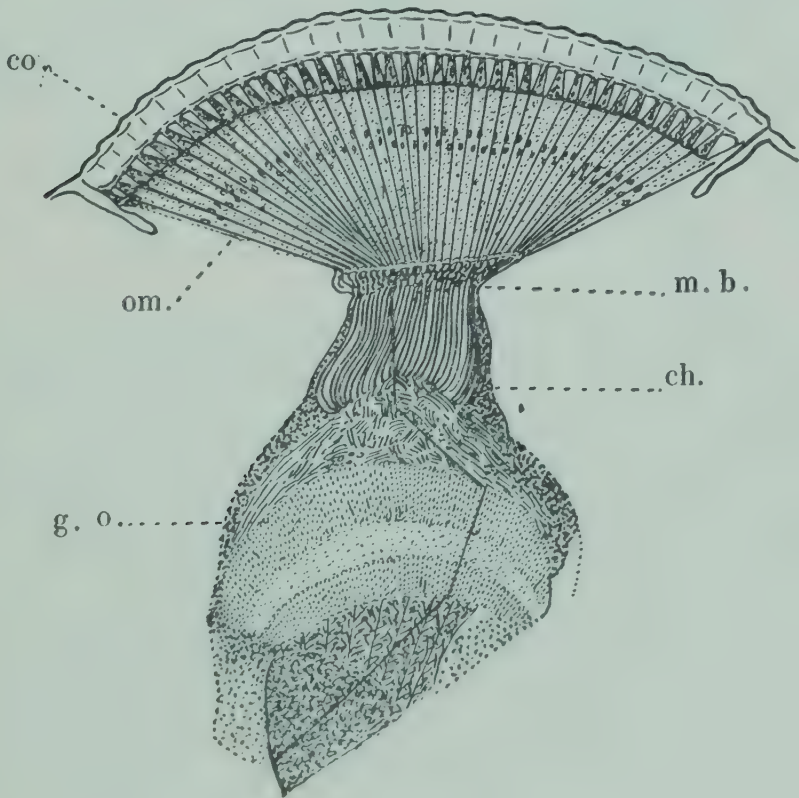


Fig. 42 - Ocellus of *Aphrophora* (Homoptera): le, corneal lens; c.p., pigmented cells (after IMMS).

Fig. 43 - Section through the compound eye of a worker-bee: co, cornea; om, ommatidia; m.b., basement membrane; ch., chiasma; g.o., optic ganglion (after IMMS).



the crystalline cone very much elongate, and not properly differentiated (Hemiptera, Diptera-Nematocera, some Coleoptera). In still other Coleoptera there are *exocone* eyes in which the true crystalline cone has been replaced by a refractile cone of cuticular origin, independent of crystalline cells.

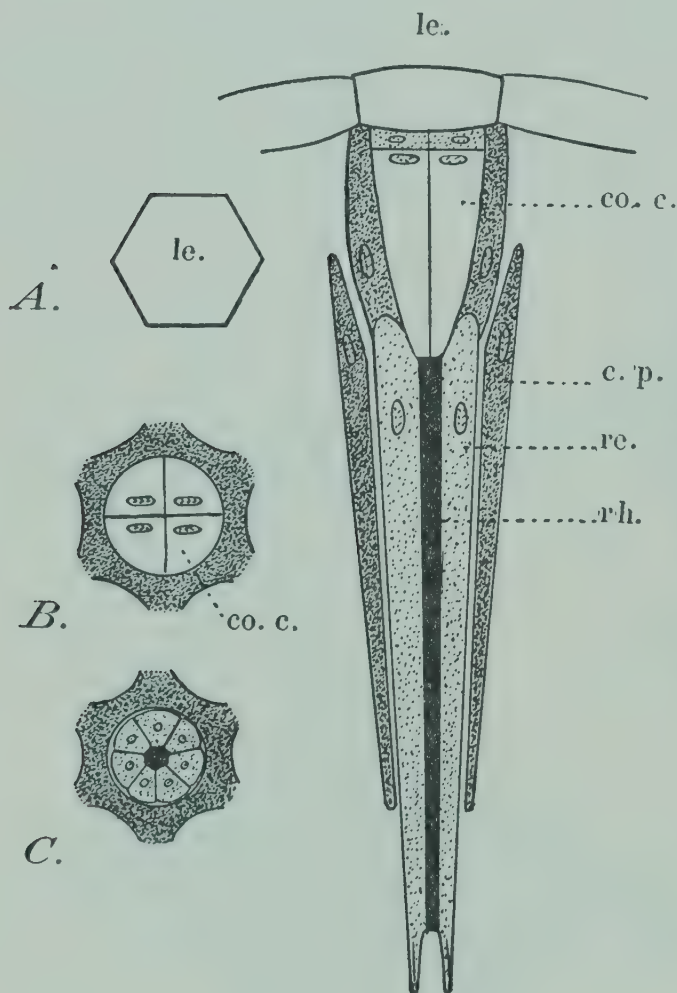


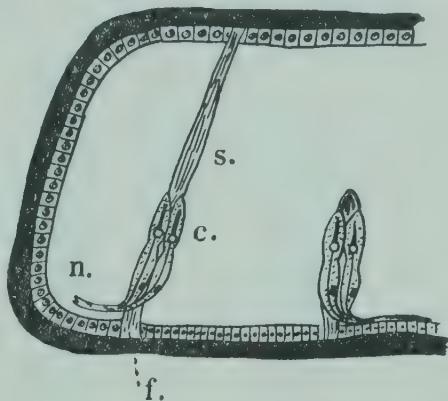
Fig. 44 – Diagrammatic cross-sections and longitudinal section of an ommatidium of a eucone eye: A, cross-section of the cornea; B, cross-section in the region of the crystalline cones; C, cross-section in the region of retinal cells. To the right, a longitudinal section. le, cornea; co.c., crystalline cones, surrounded by their generative cells; re, retinal cells; rh, rhabdome; c.p.; pigmented cells (after IMMS).

Chordotonal organs. These organs (Fig. 45), whose function seems to be to detect sounds, and also the internal vibrations produced by any disturbance in the insect's surroundings, are found in larvae as well as in adults, but they are very differently situated in the two stages. Structurally they are essentially chains of nerve-cells, of which the ends are attached to the body-wall, and which are called *scolophores*, or chordotonal organs. The simplest may be found dispersed in any part of the body. Whenever they are grouped together they form complex organs, such as the *tympanal organ* at the side of the first abdominal segment in ACRIDIDAE, or on the tibiae of TETTIGONIIDAE; or Johnston's organ, which very often occupies the pedicel of the antenna in insects.

THE REPRODUCTIVE ORGANS

In the Insecta the two sexes are separate, though there exist occasional cases of *hermaphroditism*, for example in *Icerya purchasi* (COCCIDAE). Now and then, especially in butterflies, we come across individuals which have

Fig. 45 – Types of chordotonal organ: n, nerve; s, scolophores; c, receptive cells (after IMMS).

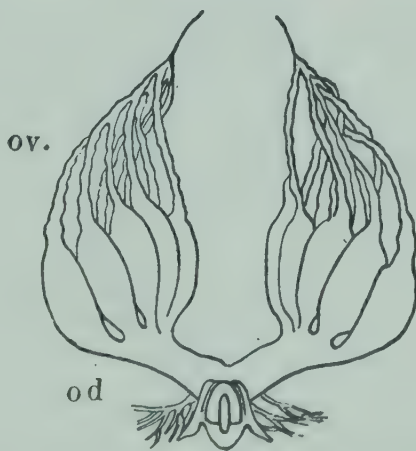


some parts of the body male, and others female: it is wrong to call these hermaphrodites, and they should be called *gynandromorphs*, since the body is a mosaic of male and female elements, with no part showing male and female characters at the same time.

Still another type is the *intersex*, in which an individual insect has begun its development as one sex, and has then changed over into the other one. This results in a different kind of mixing of the sexual characters.

The internal genital organs of insects develop from embryonic rudiments which are identical in the two sexes. Gonads develop in pairs in the mesoderm of each abdominal segment, and are linked together by two longitudinal tubules, the posterior ends of which open into one or more invaginations of the ectoderm. There is thus direct connexion between the

Fig. 46 – Genital organs of *Periplaneta* (Dictyoptera): ov, ovaries; od, oviducts (after IMMS).



glandular sex-organs and the exterior, so that the ova and spermatozoa do not have to pass through the general body-cavity.

Female organs. These consist of two ovaries and their ducts (Fig. 46). Each ovary is made up of a bundle of tubes, or *ovarioles*, varying in number,

which open separately into one of the two lateral trunks. These in turn unite into a single oviduct, opening into the *bursa copulatrix*.

Several different types of ovarioles have been described (Fig. 47). The lower insects have the *panoistic* type, in which there are no nutritive cells (*vitelline* cells) between the ova. In the two kinds of *meroistic* ovarioles, vitelline cells arise between the ova, and supply the latter with food. Where

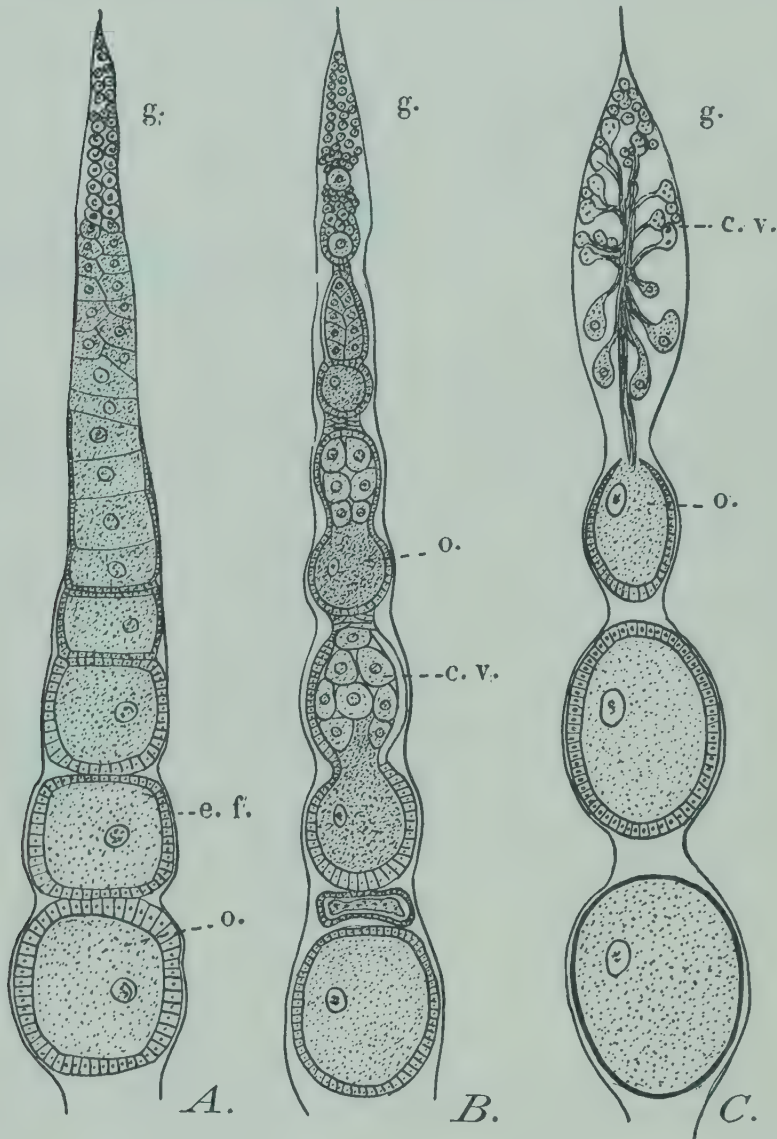


Fig. 47 – The three types of ovariole: A, panoistic; B, polytrophic meroistic; C, telotrophic meroistic. g, germarium; c.v., vitelline cells; o, ovule; e.f., follicular epithelium (after IMMS).

the vitelline cells are distributed in groups among the ova the ovariole is called the *polytrophic meroistic* type, and where they are concentrated into a *germarium* at the far end of the ovariole, this is called the *telotrophic* (or *acrotophic*) *meroistic* type.

Male organs. The testes and genital ducts of the male (Fig. 48) corres-

pond exactly to the similar parts of the female. The testes are sometimes tubular, sometimes follicular, and are continued into a *vas deferens*. The two vasa deferentia unite into a single duct, the *azygous canal*, which runs into the internal cavity of the aedeagus.

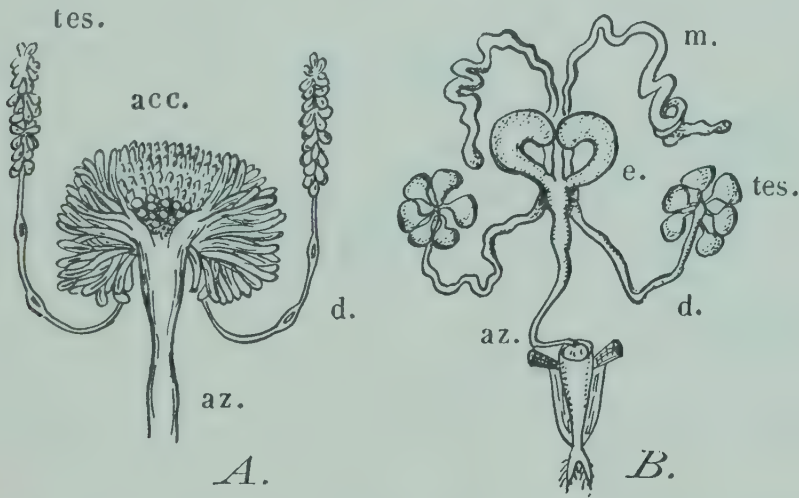


Fig. 48 – Male gonads: A, of *Periplaneta* (Dictyoptera); B, of *Tenebrio* (Coleoptera). tes., testicle; m, mesadene; e, ectadene (after IMMS).

Into the vasa deferentia there open accessory glands, known as *mesadenes*, because they are derived from mesoderm. Sometimes other accessory glands open into the unpaired duct, which is ectodermic in origin, and so they are known as *ectadenes*. All these glands secrete substances that form a capsule surrounding bundles of spermatozoa (*spermatophores*).

4

Development

EMBRYONIC DEVELOPMENT

A detailed account of the formation of the embryo, and its development up to the time of hatching from the egg, is outside the scope of this work, in which we can indicate only the most striking features of the embryology of insects.

The egg is always relatively very big, and contains a great deal of nutritive material (*vitellus*). The protoplasm is distributed round the outside of the egg (*periplasm*), while the centre is occupied by the vitellus

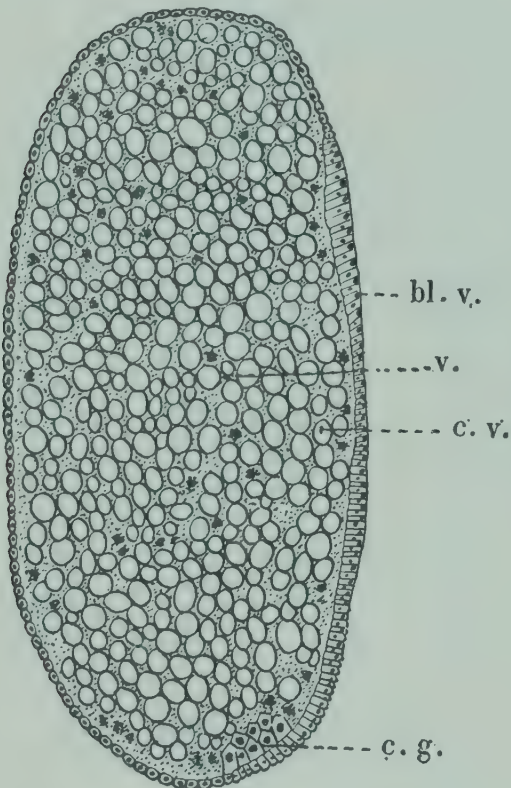


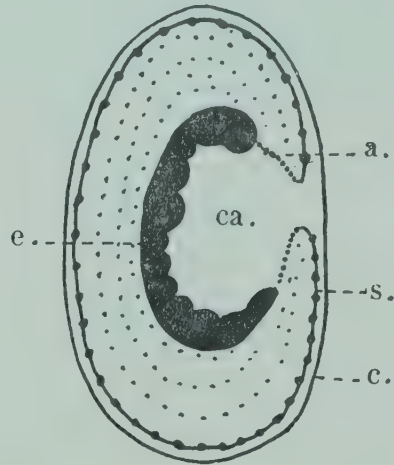
Fig. 49 – Egg of *Clytra* (Coleoptera; Chrysomelidae) at the stage when the ectoderm is formed. bl.v., ventral blastoderm; v, vitellus; c.v., vitelline cells, c.g., genital cells.

(*deutoplasm*). The segmentation of the egg is therefore located round the surface, and is called a *peripheral blastoderm* (Fig. 49).

Formation of the embryo. The embryo is differentiated from a local area of the blastoderm, called the *germ band*. During its development this does not remain on the surface of the egg, but encloses itself in a double fold of the blastoderm (*amnion* + *serosa*), and in consequence the future

embryo is surrounded by deutoplasm, from which it draws nutriment for its growth (Fig. 50). This mode of development is therefore very different from that of the vertebrates, where the segmentation is total, and the embryo arises by way of first a morula and then a gastrula.

Fig. 50 – Diagrammatic section of an embryo of *Lepisma* (Thysanura), with its envelopes. e, embryo; ca., amniotic cavity; a, amnion; s, serosa; c, chorion.



In insects we can trace the formation of three layers, *ectoderm*, *mesoderm* and *endoderm*, but here again there are profound differences from the embryos of vertebrates. The embryo moves about in the egg, turning over, and embedding itself in the deutoplasm (*blastokinesis*). On the other hand the endoderm is formed, not by an invagination of the blastoderm, but by simple proliferation from the mesodermal layer; it is far from being homologous with the endoderm of vertebrates, and some authors have doubted whether it should be recognized as an independent layer. Its only function is the formation of the mid-gut.

The stages of embryonic development. The following stages have been established by Heider, working on *Hydrophilus*, where the development takes twelve days.

FIRST STAGE—*1st day*: formation of the blastoderm. *2nd day*: metamerization of the germ band, i.e. formation of the rudiments of the body-segments; formation of the amniotic fold and of the cephalic lobe. *3rd day*: formation of the neural groove; closing of the amnion.

SECOND STAGE—*4th day*: rudiments of limbs, formation of invaginations of *stomodaeum* (mouth) and *proctodaeum* (anus). *5th day*: formation of invaginations for tracheae. *6th* and *7th days*: elongation of appendages, and of the neural groove; rupture of membranes. The mid-gut (endoderm) arises during this second stage.

THIRD STAGE—*End of 7th day*: appearance of dorsal vessel (heart), which is completely formed on the *8th day*: pigmentation of the eyes. *10th day*: tracheae become visible. *11th day*: the embryo is pigmented, and stirs beneath the chorion of the egg. *12th day*: hatching of the larva.

POSTEMBRYONIC DEVELOPMENT

Hatching. To get out of the egg, the young larva must tear the membranes that envelop it, especially the chorion of the egg, which is very tough. This is achieved in a variety of ways: either by movements inside the egg; or by means of special pulsating organs which lift a part of the chorion (Odonata); or through rents produced by the use of specially developed instruments (*egg-bursters*), such as the head-spine of PENTATOMIDAE. The young larva is active during hatching.

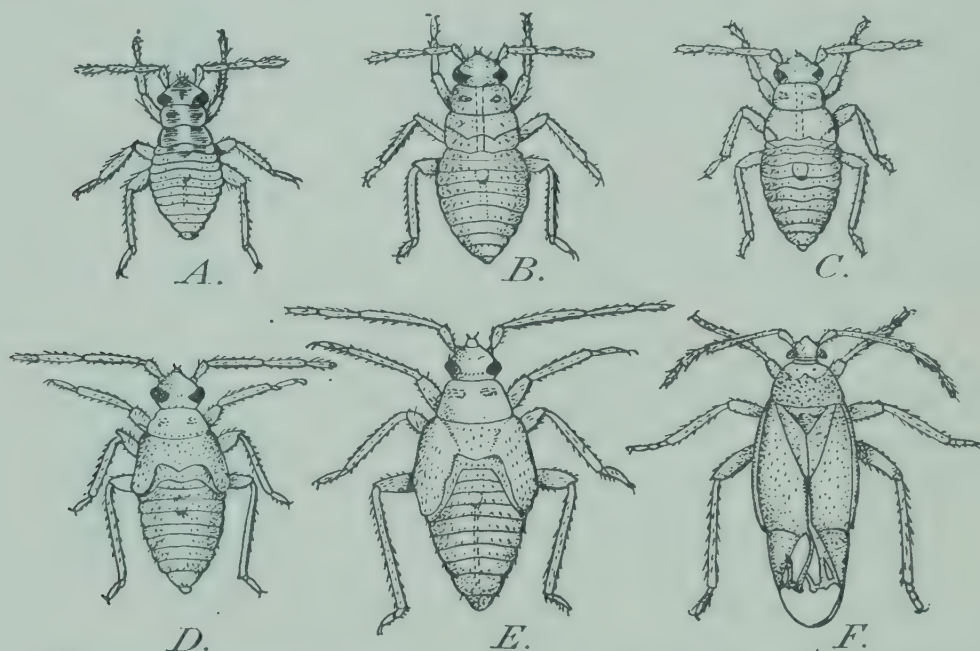


Fig. 51 – Postembryonic development of one of the Hemimetabola: *Plesiocoris rudicollis* (Heteroptera: Capsidae). A–D, larval instars; E, nymph; F, imago (after IMMS).

Metamorphosis. The lower insects, or ‘ametabola’, hatch in a form identical with that of the adult, but the great majority of insects, during their lifetime, undergo changes of appearance so great that we rightly speak of them as ‘metamorphoses’.

Insects grow in sudden steps, at the moment of moulting, when the insect is shedding its old skin (*exuvium*). The interval between two successive moults is called an *instar*. A succession of instars during which the insect preserves the same general appearance is called a ‘stage’: thus all metabolous insects pass through three stages after first emerging from the egg, larva, pupa and adult stages.

Strictly speaking there are no insects that are entirely without metamorphosis, and even in the primitive wingless insects we can detect changes during the development of an individual. In fact, there are only two groups of insects on the basis of metamorphosis: hemimetabolous and holometabolous insects.

Hemimetabola are those in which the development is progressive, punctuated by a series of moults, during which the various organs of the adult make their appearance one by one. There is no resting stage between the larva and the adult, the nymph (or stage corresponding to the pupa) being an active one, differing from the adult only in the absence of wings (Fig. 51). All kinds of variants of hemimetabolous development have been recognized and given names, which need not be listed here. The term *Exopterygota* is applied to those Hemimetabola, such as Hemiptera, which develop the wings outside the body, as wing-buds.

Holometabola (Fig. 52) are insects whose development is interrupted by a period of rest as a pupa, the insect remaining immobile (in diapause), and undergoing profound internal reorganization. The wings arise internally, as imaginal discs, and because of this we also call the *Holometabola* the *Endopterygota*.

The larva. The larva is generally mobile, and is without either wings or compound eyes. The body-cells grow as well as multiply, and become

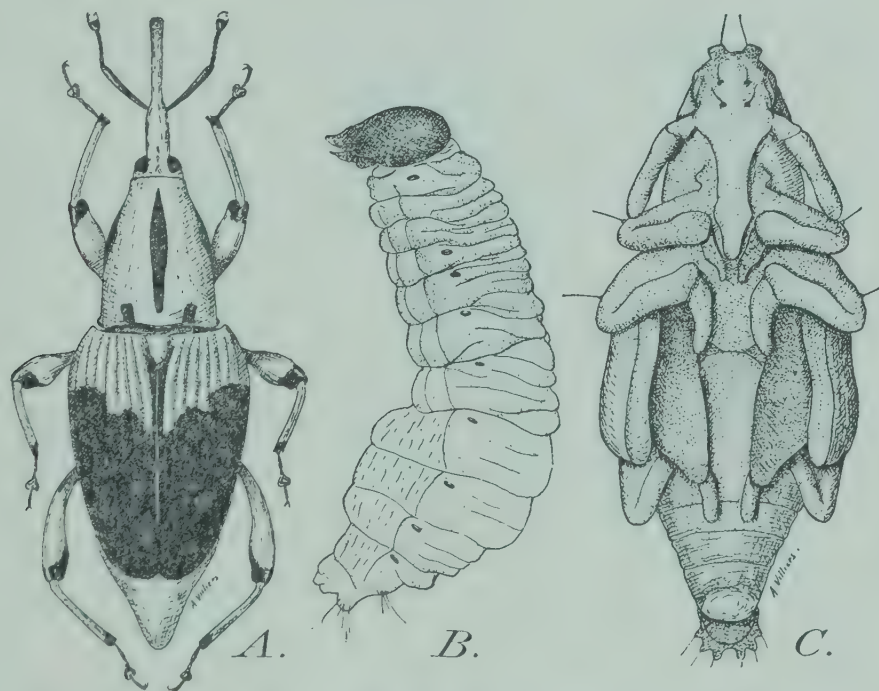


Fig. 52 – Postembryonic development of one of the Holometabola: *Metamasius sericeus* (Coleoptera: Curculionidae). A, imago; B, larva; C, pupa (after PAULIAN).

enormous compared with the size of the cells in the adult insect. The gonads appear as rudiments during larval life, but only rarely become functional.

The number of larval instars varies greatly. Some insects, notably Ephemeroptera, have a great number of instars, depending upon food, temperature and humidity, but in most insects the number is fixed. For example, most beetles have three larval instars, and nothing will alter this.

PLATE 1-III. SOME EXAMPLES OF LARVAE

- A. ***Sialis lutaria*** (Megaloptera; Sialidae). An aquatic larva (after ROUSSEAU).
- B. ***Osmyla chrysops*** (Megaloptera; Osmylidae). Terrestrial larva (after ROUSSEAU).
- C. ***Pristonychus terricola*** (Coleoptera: Carabidae). A carnivorous terrestrial larva (after BÖVING and CRAIGHEAD).
- D. ***Dineutes americanus*** (Coleoptera; Gyrinidae). A carnivorous aquatic larva.
- E. ***Elator rubricollis*** (Coleoptera: Elateridae). A larva living in wood (after BÖVING and CRAIGHEAD).
- F. ***Galeruca tanaceti*** (Coleoptera; Chrysomelidae). A phytophagous larva (after BÖVING and CRAIGHEAD).
- G. ***Hydropsyche* sp.** (Trichoptera: Hydropsychidae). An aquatic larva, living in the nests of water-rats, in East Africa.
- H. ***Sphinx convolvuli*** (Lepidoptera: Sphingidae). Caterpillar living on bind-weed (after SPULER).
- I. ***Musca domestica*** (Diptera: Muscidae). Commonly called a 'maggot' (after SEGUY).

PLATE I-III. SOME EXAMPLES OF LARVAE



Larvae also differ greatly in appearance, and attempts have been made to classify them into types. Generally speaking, the grouping of larval types does not correspond closely with the classification of the adult insects, but depends more on the way of life and the food-habits of the larvae. Pl. 1, III (A – I).

The *campodeiform* type, Pl. 1, III (C), is undoubtedly the most primitive, and in general appearance it recalls the Thysanura. These larvae are very active, either carnivorous or phytophagous, with a very well-developed

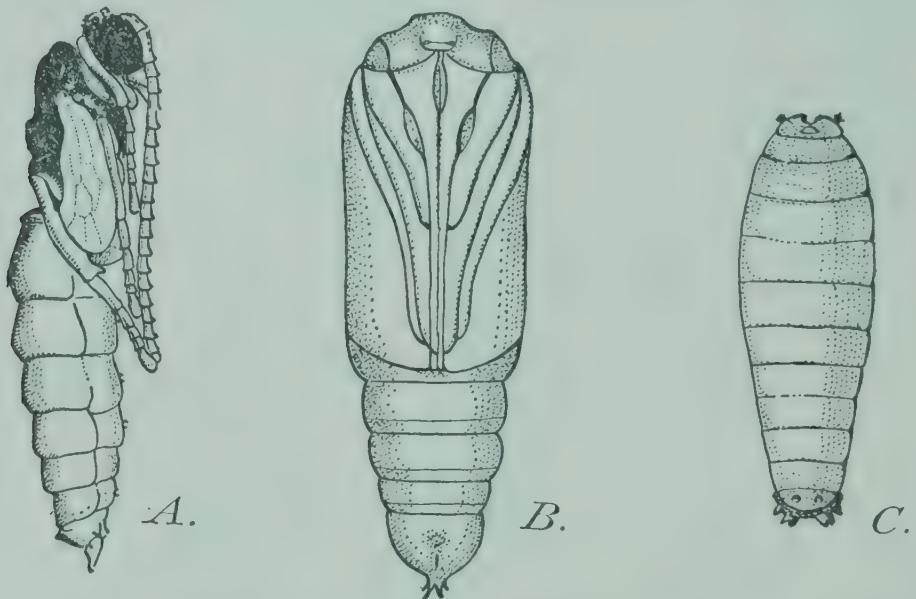


Fig. 53 – Three types of pupa: A, free pupa of Ichneumonidae (Hymenoptera); B, obtect pupa (chrysalis) of Noctuidae (Lepidoptera); C, coarctate pupa (puparium) of Muscidae (Diptera) (after IMMS).

head, mouthparts of the chewing type, long thoracic limbs, and abdomen usually with two cerci (urogomphi) on the ninth segment.

The *eruciform* type, or ‘caterpillar’, Pl. 1, III (H), is an elongate larva, cylindrical, orthognathous, with short thoracic legs, and with the abdomen often equipped with false legs (pseudopods). It is a phytophagous larva, and occurs in all Lepidoptera, as well as in Mecoptera (PANORPIDAE), and in the sawflies (Hymenoptera: TENTHREDINOIDEA).

The *apodous* type, Pl. 1, III (I), is the characteristic form of inactive, parasitic larvae, or of those that live internally in plants. It occurs in weevils and especially in Diptera, in which the head of the larva is reduced.

Many other types of larva have been described, mainly in Hymenoptera and Coleoptera, but these are either the first-stage larvae of parasitic insects, or types specialized to particular ways of feeding, and for the most part modifications of the campodeiform type.

Pupae. The pupal stage follows that of the larva, and has rudiments of wings. In higher insects (Holometabola) the pupa is inactive, and does

not feed; in these insects it is a critical period, during which all the larval tissues and organs dissolve, and are replaced by those appropriate to the adult, which are often very different. These internal changes begin after the end of the larval life, in an interval known as the prepupa.

Pupae may be *free* (Hymenoptera; Coleoptera), that is to say the wings and limbs are not stuck down to the body, and the pupa has at least the possibility of movement (Fig. 53 *A*). *Obtect* pupae (Fig. 53 *B*) have the wings and appendages stuck down to the body by an adhesive produced during the last moult. The chrysalis of Lepidoptera is of this type. Yet a third type is the *coarctate* pupa (Fig. 53 *C*) of Diptera in which the skin of the third-stage larva is retained as a puparium, and immobilizes the insect completely.

Finally, pupae are often protected by a cocoon of silk secreted by the larva during its last instar. Cocoons are found in many Orders of insects, more especially in Neuroptera, Lepidoptera, Trichoptera, and Hymenoptera-Tenthredinoidea. To emerge from the cocoon the adult insect makes use of its mandibles, at least in Neuroptera, Trichoptera and *Micropteryx*, all of which have mandibles in the pupa. In Lepidoptera other than *Micropteryx* emergence is helped by temporary organs on the head or at the base of the wings, and also by solvent secretion.

The adult (imago). The imago, or perfect insect, is characterized by the presence of wings, and by having the gonads matured and ready for reproduction. The gonads are the only organs to persist right through from the larva; all other organs of the adult are new structures, developed from *imaginal buds* during the pupal stage. In the adult organs that arise in this way the cells remain fixed, and do not afterwards grow, either in size or in number.

The imago is often very different from the larva, and possesses organs of a different type, often more advanced. As a general rule they do not mature any further, except in some primitive Palaeoptera, such as the Ephemeroptera. These leave the water and take wing as a *subimago*, and settle on the ground or on vegetation before they moult for the last time, and shed their subimaginal skin.

Hypermetamorphosis. This term is used when an insect changes its structure and habits in different larval instars. In many beetles the first instar larva (*larvule*) differs from the subsequent ones in definite morphological details, but hypermetamorphosis is more generally associated with species that have some kind of abnormal habits, especially with parasites.

Take the case of the MELOIDAE, the blister-beetles. Their larvae are parasites either of the egg-cases of grasshoppers, or of the eggs, larvae and food-reserves of bees, but they also occur on many predatory insects as well. For example *Sitaris muralis*, a parasitic on bees of the genus *Anthophora*, has the following stages (Fig. 54):

1. Primary larva, or *triangulin*, a little campodeiform larva which emerges from its egg and then lies in wait for an *Anthophora*, attaching itself to the hairs of the bee in order to be carried to the nest. The triangulin lets go and falls into a cell of the nest at the moment when an egg is laid in it by the bee. Sealed in the cell, the beetle-larva feeds upon the egg, and upon the food stored there for the use of the expected bee-larva.

2. Secondary larva is ovoid, with very much reduced limbs. It floats on the honey filling the cell, and eats it. It moults twice, and when all the honey is gone, contracts, and turns into a *pseudopupa*, without distinct appendages, but with well-developed spiracles.

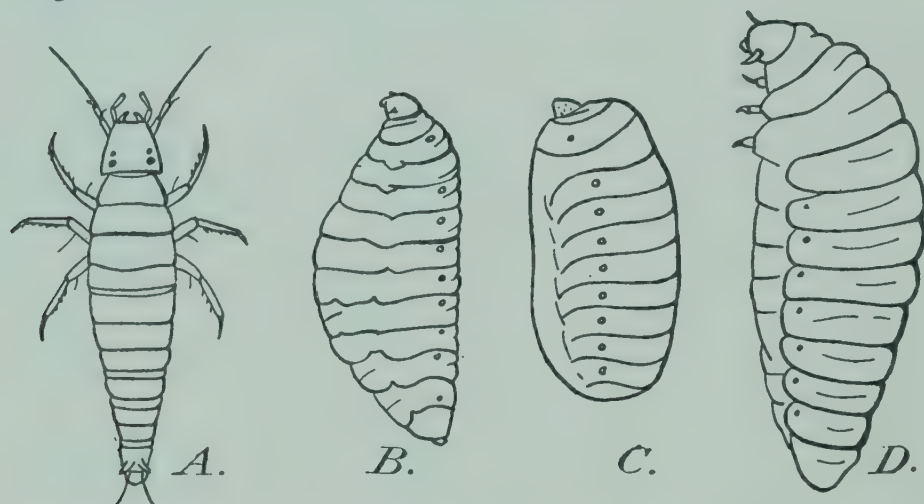


Fig. 54 – Hypermetamorphosis: the four larval instars of *Sitaris muralis* (Coleoptera: Meloidae). A, triangulin; B, second larval form; C, pseudopupa; D, tertiary larva (after PAULIAN).

3. Tertiary larva or *prepupa*, resembles the secondary larva, but has the appendages even more reduced, and the integument less strongly sclerotized. This larva takes no food, and in a short time transforms into the *pupa*, from which the adult emerges.

Thus, counting the three instars of the secondary larval stage, there are nine stages from egg to adult inclusive.

Many other insects are known to undergo hypermetamorphosis at least as complicated as that of *Sitaris*.

DEVELOPMENTAL ANOMALIES

Modifications of the normal life-cycle, such as we are about to describe, are by no means rare. The principal ones are:

Parthenogenesis. Reproduction taking place without fertilization, and known as *arrhenotokous* parthenogenesis when it produces males only, and *thelytokous* when only females occur. *Sporadic* parthenogenesis is that which may be brought on irregularly from some external cause, and may give rise to either sex.

Some species are exclusively parthenogenetic. The thelytokous type is

constant among CYNIPIDAE or CHALCIDIDAE (*Aphelinus*), Thysanoptera, Homoptera (ALEUROIDIDAE), Coleoptera, and Phasmida. The males are rare, or quite unknown, and the species propagates itself by females only for many generations. *Cyclic* parthenogenesis, in which sexual generations alternate with parthenogenetic ones, occurs in many groups, notably among APHIDIDAE and CYNIPIDAE. Here there are two distinct types of female, which arise in response to the appropriate environmental conditions.

Polyembryony. P. Marchal discovered this mode of reproduction. In the first period of segmentation of the egg the blastomeres, the first few cells produced, separate from each other and give rise to the same number of separate embryos. In some small Hymenoptera, parasitic on caterpillars (*Hyponomeuta*), such as *Ageniaspis fuscicollis*, a single egg may in this way give rise to several hundred individuals, all of the same sex.

Viviparity. Normally, insects lay eggs, but it is not rare for the female to retain the eggs until after they have hatched. All stages can be found between ovoviviparity and viviparity in the true sense. For example, many flies drop larvae, and Diptera-Pupipara, some of which parasitize bats, drop fully matured larvae, which immediately pupate.

Paedogenesis. This is reproduction by insects while they are still in the larval state, as a result of the premature development of the gonads. Paedogenetic insects are not usually impregnated, but produce their eggs parthenogenetically. Paedogenesis, which is the state of being able to reproduce while still a larva, should not be confused with **neoteny**, which means retaining some larval characters after becoming an adult.

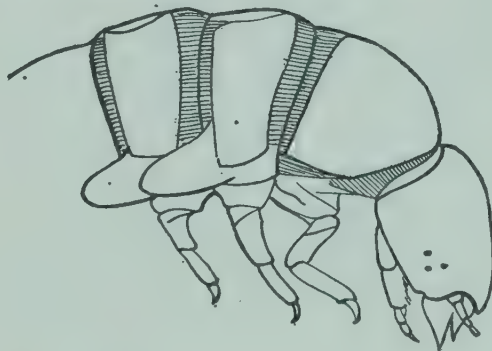


Fig. 55 – Prothetelic larva of *Tenebrio molitor* (Coleoptera), showing rudiments of wings (after PAULIAN).

Prothetely. Quite often when bred artificially, but more rarely in nature, insect larvae may have rudiments of wings, which have matured at a greater rate than the rest of the body. This occurs only in insects that have many and varied larval instars, as in the beetle *Tenebrio molitor* (Fig. 55).

Foetometamorphosis. This term is applied to certain insects which emerge from the egg as an embryonic prelarva, with rudimentary appendages, and then immediately moult into a true larva. This is known in MANTIDAE and in beetles of the family CANTHARIDAE.

5

A General Classification of the Insects

UNTIL about the end of the last century the classification in general use was still very nearly that of Linnaeus. Two Orders, Orthoptera and Thysanoptera, had been added to the seven Linnean ones, making a total of nine, as follows:

1. **Aptera** (without wings). Chewing mouthparts. Rudimentary metamorphosis.

2. **Orthoptera** (straight wings). Four wings, the fore-wings leathery. Chewing mouthparts. Incomplete metamorphosis.

3. **Neuroptera** (wings with prominent veins). Four membranous wings, often with a network of veins. Chewing mouthparts. Metamorphosis variable.

4. **Hymenoptera** (membranous wings). Four wings, with the venation reduced, the second pair not folded away when at rest. Mouthparts of the chewing type, but often also with a sucking proboscis. Metamorphosis complete.

5. **Coleoptera** (wings encased). Four wings, the fore pair converted into wing-cases (elytra), the hind pair folding away under them. Chewing mouthparts. Complete metamorphosis.

6. **Lepidoptera** (wings with scales). Four large wings covered with scales. Sucking mouthparts. Complete metamorphosis.

7. **Diptera** (two wings). A single pair of membranous wings. Sucking mouthparts. Complete metamorphosis.

8. **Thysanoptera** (fringed wings). Four very narrow wings, with fringes of long hairs. Mouthparts imperfectly adapted for sucking. Complete metamorphosis.

9. **Hemiptera** (half-wings). Four wings, of which the fore pair may be half-leathery, half-membranous, or entirely membranous. Sucking mouthparts. Incomplete metamorphosis.

This system was far too simple, and was far from providing a natural classification. Insects without any real relationship were placed in the same Order. It was generally realized that the wingless insects did not all belong to the Order Aptera, and that this should be limited to the Thysanura and Collembola, removing from it the fleas and lice and other insects which are wingless as a result of secondary degeneration. Orthoptera brought together a diverse collection of families, while Neuroptera

included hemimetabolous insects, like the dragonflies, and holometabolous insects like the ant-lions, the scorpion-flies and *Sialis*.

So attempts were made to increase the number of Orders of insects. Packard (1886) recognized fifteen, and almost simultaneously Brauer (1885) raised the number to sixteen. The classification of Brauer was a considerable step forward. This German author contrasted the Pterygota with the Apterygota, and emphasized the fundamental differences between these two groups. Within the Pterygota he made a number of natural subdivisions, taking into account not only the structure of the wings and of the mouthparts, but also the number of Malpighian tubules, the evolution of the prothorax, and the embryology.

The main lines of a really natural classification of insects have been laid down only recently, following upon discoveries in palaeontology. It had to wait until the remains of the insects of the past showed up the true relationships of the insects of the present. The recent work of Handlirsch, Lameere, Tillyard, and Martynov has made possible a classification of insects that includes both the extinct and the living forms.

A first attempt at such a system was propounded by Lameere in his *Précis de Zoologie* (1931), but he did not give a systematic arrangement into Orders and Sub-orders. Lameere's system, modified and perfected by incorporating the ideas of the Russian entomologist, Martynov, was adopted in Vol. VIII of the *Traité de Zoologie* (Ed. P.-P. Grassé: Paris. Masson et Cie), and is briefly summarized here.

THE MAJOR DIVISIONS

The classification of insects is based principally upon the segmentation of the body, on the presence or absence of wings, and on their structure. Four Sub-Classes are recognized.

Three of these are composed of primitive forms, which have never developed wings, and which on older classifications were grouped together as *Apterygota*. We have already seen that these *Apterygota* are in fact a mixed group, and that the Collembola, Protura and Thysanura differ greatly in the way that the segmentation of the body is developed. Collembola are Protomorpha, Protura are Anamorpha, and Thysanura are Epimorpha, and we must raise them to the rank of three Sub-Classes.

This leaves all the winged insects, which all belong to the Epimorpha and which make up the great majority of all insects. To subdivide this group we make use of divergences that arose very early in the evolution of wings, and which it is convenient to recapitulate here.

The Evolution of Wings

The earliest insects must have had, all along the body, plate-like extensions of the terga (*nota*) of the segments, traces of which can still

be seen in many larval insects (Fig. 56) and in some Thysanura, such as *Lepisma*. These organs, more highly developed on the thoracic segments, must at first have been rigid planes, which helped arboreal insects to glide from one branch to another; later on these planes became modified into membranous structures supported by stiff veins. At first the wings must have projected horizontally out of the sides of the body, but as they became bigger and more flexible, and developed articulations with the thorax, they were able to beat up and down, and so to produce true flight. This stage had certainly been reached by the Devonian period, 450 million years ago.

There then arose a divergence in the evolution of the wings. Some insects still held the wings at rest in a horizontal plane, as do the Odonata, and these are called the **Palaeoptera**, since they keep their wings in the primitive position. Many others modified their wings beyond the mere requirements of flight, and folded them back, so that the fore pair could be adapted as a shield for the hind pair. The hind-wings, on the other hand, increased their lifting surface by expanding the *jugal field* as a membranous fan, called the *neala* by Martynov. The name **Neoptera** is used for these insects which fold their wings backwards when at rest, and which have a more or less highly developed 'new wing'.

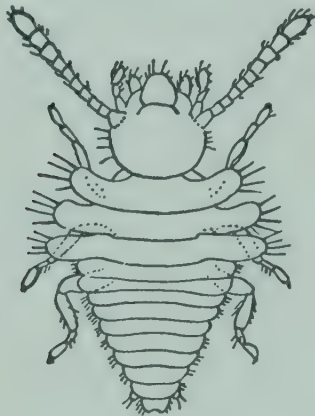


Fig. 56 – Larva of *Calotermes* (Isoptera), with large paranotal lobes on the thoracic segments (after IMMS).

Early in their evolution, in the Palaeozoic, the two types—Palaeoptera and Neoptera—existed in about equal proportions, but in recent times the Palaeoptera (Ephemeroptera and Odonata) have dwindled in numbers, and the very great majority of winged insects today are Neoptera. Within the Neoptera we can separate groups according to the development of the jugal field: *Polyneoptera*, *Oligoneoptera* and *Paraneoptera*. These groups are classified, not only on their wing-structure, but also on the consensus of characters, on life-history, and on metamorphosis.

Thus the Sub-Class Pterygota, comprising more than a million living species, can be arranged in four divisions according to the evolution of the wings: Palaeoptera, Polyneoptera, Oligoneoptera and Paraneoptera,

the last three being themselves subdivisions of the Neoptera. These four divisions contain 40 Orders of insects, 32 of which have living representatives, the other 8 being known only as fossils.† However we look at it, we have gone a long way from the 9 Orders of a century ago.

Sub-Class *COLLEMBOLA*

Tiny insects, without wings and without a metamorphosis, of a proto-morphous type—that is, with the body developed from only nine post-cephalic segments. Mouthparts at the bottom of a buccal cavity (*endotrophic*), 3–6 segmented antennae, and a postantennal organ of unknown function. Abdomen six-segmented, with segmental appendages (abdominal legs) modified into a jumping organ. Genital opening on the fifth abdominal sternite.

A single Order:

1. Order **Collembola**. Pl. 1, IV (A, B, C). This Order has existed since the Devonian, and at the present time is represented by several thousand species in a number of families. Collembola live in vegetable detritus, in moss, under bark and under stones. Some species are found by the water's edge, on the seashore, and in the mountains; certain species inhabit glaciers, and there are many in the Arctic.

The Arthropleona (PODURIDAE) are of elongate shape, with the abdominal segments distinct, and without tracheae. Some of them (ANURIDAE) do not jump.

The Actaetoidea (*Actaetes*) also have the abdominal segments distinct, but in other respects resemble the following.

The Symphypleona (SMINTHURIDAE) are of very small size, short and squat, with a big head, and a round and unsegmented abdomen. There is a tracheal system.

Sub-Class *PROTURA*

Anamorphous insects of the smallest size, and wingless. At the start of larval life they have only eight abdominal segments, and only attain the full number of twelve when they become adult. Mouthparts entotrophic. No antennae. The first few abdominal segments bear the rudiments of legs, and there are rudimentary Malpighian tubules. The genital opening is on the eleventh abdominal sternite.

A single Order:

2. Order **Protura**. Pl. 1, IV (D). These insects remained unknown for a long time, because of their very small size. Nevertheless they are very common, and widely distributed in humus and vegetable debris. About fifty species are known, all predaceous, and divided between two families.

EOSONTOMONIDAE have both spiracles and tracheae; ACERENTOMONIDAE have neither.

PLATE 1 – IV. PRIMITIVE WINGLESS INSECTS (APTERYGOTA)

A. *Podura aquatica* (Arthropeona: Poduromorpha) (after WILLEM).

B. *Tomocerus plumbeus* (Arthropleona; Entomobryomorpha)
(after WILLEM).

C. *Sminthurus aquaticus* (Symphypleona; Sminthuridae)
(after WILLEM).

ORDER PROTURA

D. *Acerentomon doderoi* (Acerentomonidae) (after SILVESTRI).

ORDER THYSANURA: ENTOTROPHA (or DIPLURA)

E. *Campodea staphylinus* (Campodeidae) (after LUBBOCK).

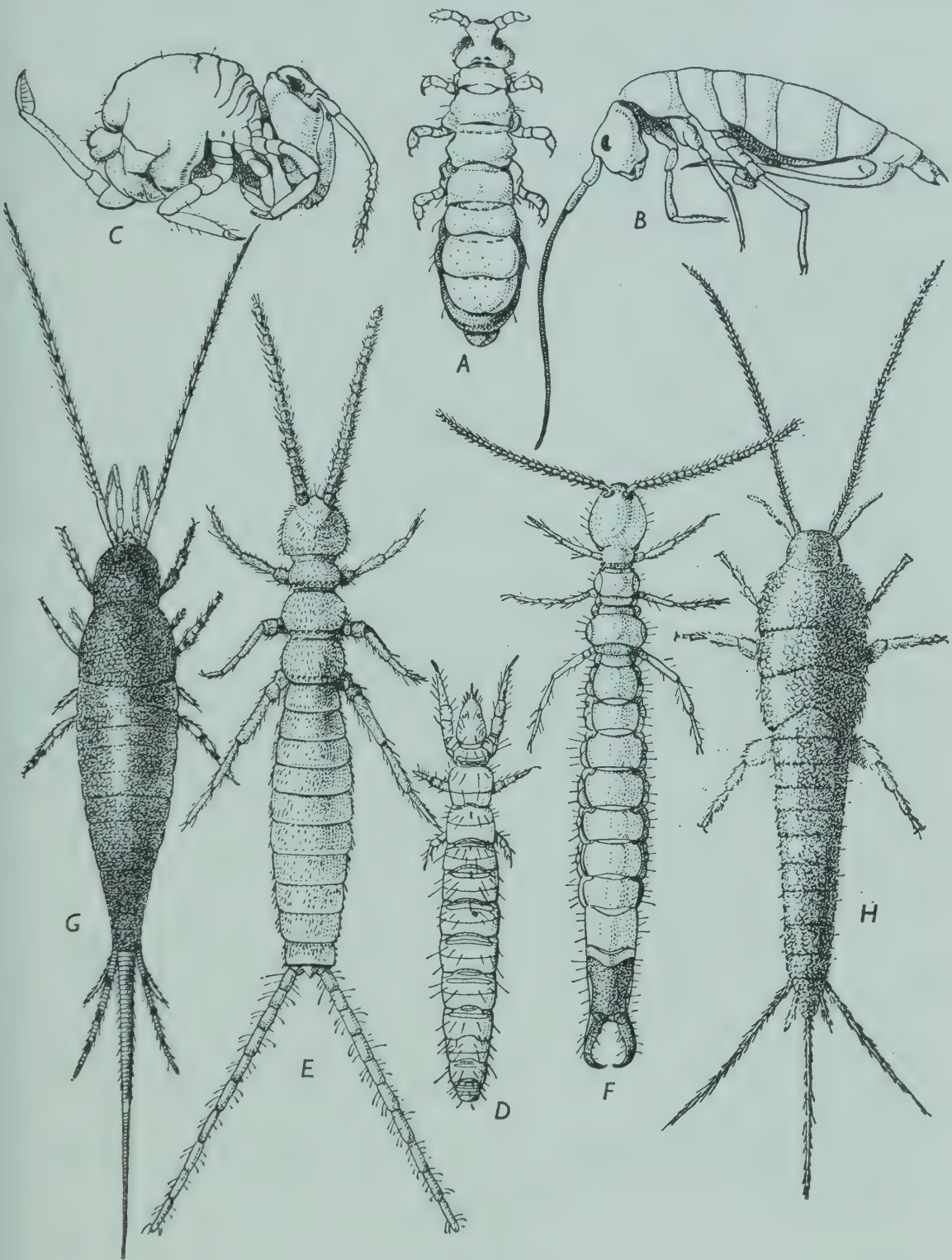
F. *Japyx solifuga* (Japygidae) (after LUBBOCK).

ORDER THYSANURA; ECTOTROPHA

G. *Machilis polypoda* (Machilidae) (after LUBBOCK).

H. *Lepisma saccharina* (Lepismidae) (after LUBBOCK).

PLATE 1 - IV. PRIMITIVE WINGLESS INSECTS (APTERYGOTA)



Sub-Class *THYSANURA*

These are still Apterygota, but of the epimorphous type; the number of abdominal segments is fixed at twelve from the embryo onwards. There are segmented antennae, and abdominal cerci on the eleventh segment.

3. Order **Entotropha**. Pl. 1, IV (E, F). The entotrophic Thysanura (or Diplura) have their mouthparts placed at the bottom of a cavity; the body segments have no paranotal lobes; the tarsi have a single segment.

About 150 species are known, living in temperate and tropical countries. The principal genera are *Campodea* and *Japyx*.

4. Order **Ectotropha**. Pl. 1, IV (G, H). Mouthparts freely exposed; compound eyes; paranotal lobes; tarsi with two or three segments. The last abdominal segment bears a long, unpaired median process between the two cerci. Body covered with scales.

About 350 species. The genus *Machilis*, laterally compressed, uses its cerci as jumping organs. *Lepisma* and *Nicoletia* are dorso-ventrally flattened, and do not jump, but run rapidly among stones. Some of this group live with ants.

Sub-Class *PTERYGOTA*

These have also been called Pterygogenea (Handlirsch) and Ptilota (Lameere). They have wings in the adult state, or if wings are not present we can easily confirm that they arise from winged ancestors, and have lost the wings by secondary degeneration. The number of segments in the whole body is fixed at twenty-one, and the larvae show traces of characters reminiscent of the ectotrophic Thysanura.

In order to have wings in their adult state, these insects have to undergo metamorphosis from a wingless larva, but the severity of the metamorphosis varies a good deal. Many species have larvae that are not different from the adult except in the absence of wings: these are the *Hemimetabola*. In contrast, the *Holometabola* have a larva that is very different from the adult, and use an immobile pupal stage to bridge the gap. In both these groups a variety of types of metamorphosis have been described.

The Sub-Class Pterygota includes the great majority of all insects, recent and fossil, and dates back to the middle Carboniferous.

A. SECTION PALAEOPTERA

Palaeoptera, or insects with primitive wings, are those in which the wings are normally carried stretched out sideways, both in flight and at rest, and are not folded backwards. Sometimes, as in Ephemeroptera and Zygoptera, the wings are carried vertically when at rest, with the dorsal

surfaces pressed together, but the fore-wings never cover the hind ones. There is no jugal field of the wing.

Superorder PALAEODICTYOPTERA

These were the most primitive of the Palaeoptera, and were of large size, heavily built, with their organs very little specialized, and homonomous, that is not differentiated, but all made from rather similar components. Many of them had prothoracic lobes, rudiments of a third pair of wings. The larvae were aquatic. They became extinct at the end of the Palaeozoic.

5. †Order **Eupalaeodictyoptera**. Phytophagous or saprophagous insects with chewing mouthparts. Abundant in the Carboniferous.

6. †Order **Protohemiptera**. *Eugereon böckingi*, looking like a dragonfly with the proboscis of a bug, occurs in the Permian of Germany, and sucked vegetable juices. It is not a direct ancestor of the present Hemiptera, which are derived from quite a different stock.

7. †Order **Megasecoptera**. Rather like the Eupalaeodictyoptera but of a more slender shape, and carnivorous, chasing their prey in the air, like the modern dragonflies. This Order, in which is included the Protohymenoptera, flourished in the Permian. Here again, the Protohymenoptera are not ancestors of the modern Hymenoptera and their name is based upon superficial similarities of venation between the two groups.

Superorder EPHEMEROPTERA

8. †Order **Protephemeroptera**. A strange insect, *Triplosoba pulchella*, known from the Upper Carboniferous of Commeny, looks like a mayfly, but has two similar pairs of wings. For this reason it is put into a separate Order, slightly off the direct line of ancestry of the mayflies.

9. Order **Plectoptera**. Pl. 1, VII (1, 2). This consists of the true mayflies, in which the hind-wings are always different from the fore-wings. The first members appear in the Permian.

Mayflies are recognizable at sight from their habit of holding the wings erect, not folded backwards, and by having two or three 'tails' (a pair of cerci and a median paracercus). The wings have many longitudinal veins, and a great many cross-veins, thus dividing the membrane into a large number of small cells. The larvae are aquatic, living in streams and brooks. Like the adult, the larvae also have 'tails', and tracheal gills. There are many larval moults before wing-buds appear (nymphal stage), and the first winged stage (subimago) moults yet again after leaving the water (imago).

The mayflies may be put into a single family, EPHEMERIDAE, with more than 500 species.

PLATE 1 – V. PTERYGOTE INSECTS (POLYNEOPTERA),
including a number that are secondarily wingless

ORDER ISOPTERA

A. **Archotermopsis wroughtoni** (Termitidae). Winged male
(after IMMS).

B. **Termes spinosus** (Termitidae). Big-headed soldier
(after DESNEUX).

ORDER ZORAPTERA

C. **Zorotypus hubbardi**. Winged female (after CAUDELL).

D. **Zorotypus guineensis**. Apterous female (after SILVESTRI).

ORDER NOTOPTERA

E. **Grylloblatta campodeiformis** (Grylloblattidae), from North
America (after CHOPARD).

ORDER EMBIOPTERA

F. **Embia sabulosa** (Embiidae). Apterous female (after ENDERLEIN).

ORDER DERMAPTERA

G. **Bormansia africana** (Forficulidae). Male, from East Africa
(after ALLUAUD and JEANNEL).

H. **Hemimerus talpoides** (Diploglossata). Parasite of the Giant
Rat (*Cricetomys gambiensis*) in Africa (after CHOPARD).

I. **Arixena esau** (Arixenoidea). Parasite of bats in India
(after CHOPARD).

PLATE 1 - V. PTERYGOTE INSECTS (POLYNEOPTERA),
including a number that are secondarily wingless

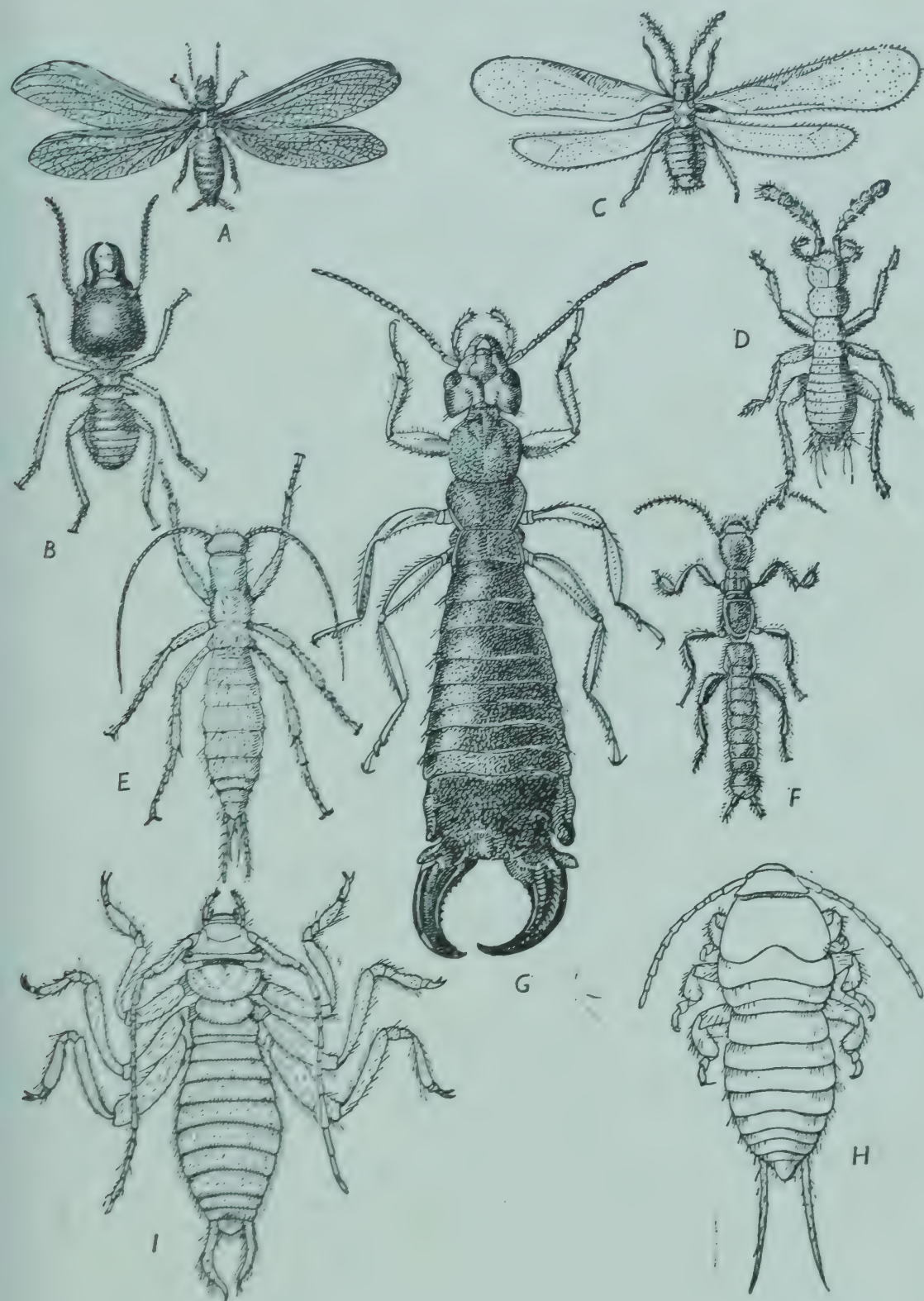


PLATE 1 – VI. PTERYGOTE INSECTS (OLIGONEOPTERA
AND PARANEOPTERA)

ORDER SIPHONAPTERA

A. **Mesopsylla eucta** (Pulicidae). A flea on the jerboa (after DAMPF).

ORDER STREPSIPTERA

B. **Eoxenos laboulbenei** (Mengeidae). Winged male, parasite of
Lepismidae (after PARKER and SMITH).

ORDER PSOCOPTERA

C. **Atropos pulsatorius** (Psocidae) (after ENDERLEIN).

ORDER MALLOPHAGA

D. **Trichodectes vulpes**. Female, parasite of the wolf (after KELLOY).

ORDER ANOPLURA

E. **Pediculus vestimenti**. The Body Louse (after MÜLLER).

ORDER THYSANOPTERA

F. **Limothrips poophagus**. Winged male (after HINDS).

ORDER HOMOPTERA

G. **Cicadula sexnotata** (after WEBER).

ORDER HETEROPTERA

H. **Graphosoma lineatum** (Pentatomidae) (after WEBER).

I. **Cimex lectularius** (Cimicidae). The Bed-Bug (after WEBER).

PLATE 1 - VI. PTERYGOTE INSECTS (OLIGONEOPTERA
AND PARANEOPTERA)

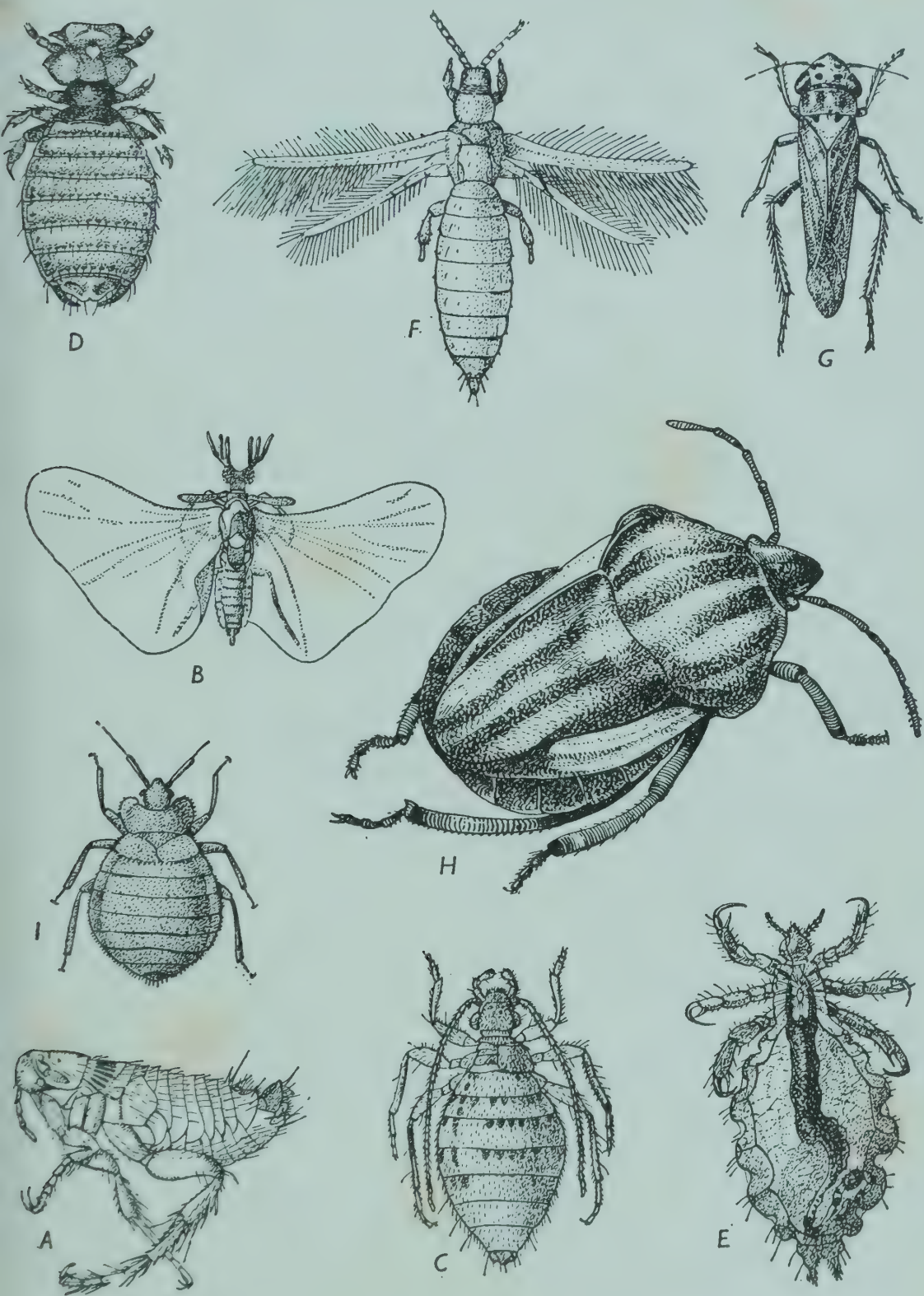


PLATE 1 – VII. PTERYGOTE INSECTS (PALAEOPTERA
AND POLYNEOPTERA)

ORDER PLECOPTERA

1. *Ephemera vulgata* (Ephemeridae).
2. Larva of a Ephemerid.

ORDER ODONATA

3. *Onychogomphus forcipatus* (Anisoptera).
4. Larva of *Aeschna* (Anisoptera).
5. Larva of *Libellula* (Anisoptera).
6. *Calopteryx virgo* (Zygoptera).
7. *Agrion pulchellum* (Zygoptera).
8. Larva of *Agrion* (Zygoptera).

ORDER PLECOPTERA

9. *Platynemesis pennipes* (Perlidae).

(All European.)

VII





PLATE 1 – VIII. PTERYGOTE INSECTS (POLYNEOPTERA)

ORDER DICTYOPTERA

1. *Pseudophoraspis nebulosa* (Blattidae).
2. *Creoboter gemmatus* (Mantidae).

ORDER CHELEUTOPTERA

3. *Phyllium bioculatum* (Phasmidae).
4. *Trachythorax maculicollis* (Phasmidae).

ORDER ORTHOPTERA

5. *Homorocoryphus cornatus* (Tettigoniidae).
6. *Aularches miliaris* (Acridiidae).
7. *Gymnogryllus elegans* (Gryllidae).

(All from tropical Asia.)

Superorder ODONATOPTERA

Here again we have two Orders, one extinct and one existing.

10. †Order **Meganisoptera**. These were insects of gigantic stature resembling enormous dragonflies. *Meganeura monyi*, found at Commeny, a fine impression of which is on view in the Paris Museum, had a wing-span of 70 cm.

The Meganisoptera became extinct in the Permian, leaving no descendants.

11. Order **Odonata**. Pl. 1, VII (3–8). The Odonata are not descended directly from the Meganisoptera, but arose in a parallel line during the Permian. They are distinguished by the evolution of the wings, which have a pterostigma (a dark spot on the anterior border), and other characters such as the nodus and the arculus. *Anisoptera* (*Aeschna*, *Libellula*) hold their wings out horizontally when at rest, while *Zygoptera* (*Agrion*, *Clopteryx*) hold them erect, pressed back-to-back, but not folded posteriorly.

Odonata are carnivorous, and have aquatic larvae, which are notable for the *mask*, an organ for seizing prey, built up from the various parts of the labium. P. 1, II (A).

There are very many species, belonging to 400 genera, which themselves are arranged in three sub-orders: Anisoptera, Zygoptera, and Anisozygoptera. The last of these flourished in the Jurassic, but at the present day is known only from two Asiatic species.

B. SECTION POLYNEOPTERA

These are Neoptera (i.e., insects which fold their wings backwards when at rest, the hind-wings having a jugal field), in which the fan-like jugal field is highly developed, and supplied with a great number of veins (Fig. 21). The two pairs of wings are quite independent of one another, without any form of coupling device. With the exception of some termites, all the insects of this section have numerous Malpighian tubules, from 8 to 60 (Polynephridia). They are all hemimetabolous.

Superorder BLATTOPTEROIDEA

In this group the wing-venation is primitive, and the tarsi of the legs always five-segmented. There are four Orders of which only one, *Protoblattoptera*, is extinct.

12. Order **Dictyoptera**. Pl. 1, VIII (1, 2). This Order is composed of the cockroaches and the mantids, which seem to be closely related in spite of striking differences in appearance and habits. They have in common a similar wing-venation, multi-segmented cerci, and the habit of laying eggs in ootheca. The early stages are terrestrial.

Cockroaches were abundant in the Palaeozoic, and are one of the most ancient groups of living insects. They dislike the light, and feed on decaying organic matter. At the present time there are nearly 2,500 species known, mostly in the tropics.

Mantids are very slender in shape, and live in the sun, chasing living prey. They have prehensile fore-legs, and the head can turn in any direction. Some of them closely resemble foliage or flowers both in form and colour. There are more than 1,500 species of mantids in warm countries.

13. †Order **Protoblattoptera**. The Protoblattids lived in the Carboniferous and the Permian. They had the venation of the Blattids, but presented a different appearance because of the prothorax, which was always narrow, and did not cover the head. Far from shunning the light, as cockroaches do, the Protoblattids undoubtedly lived in trees.

14. Order **Isoptera**. Pl. 1, V (A, B). The termites are evidently related to the cockroaches and the Protoblattids, but they have evolved into social insects, of quite a different appearance from these. They have the five-segmented tarsi of the cockroaches, and the primitive termites of the family **MASTOTERMITIDAE** link with the cockroaches by means of their wing-venation and the numerous Malpighian tubules.

The sexes are very different, and there are also several castes, asexual forms, workers, soldiers, with a variety of strange characters: deformed mandibles, swollen heads, snouts, etc. Workers and soldiers are wingless; the sexual forms have wings, but lose them immediately after the nuptial flight. Blind, and shunning the light, termites live in the ground or in wood which they are able to digest. Some make use of symbiont Protozoa in the gut to break down cellulose, but others do so by a process that is still unexplained. There are about 1,200 species, many of which erect the nests that are so conspicuous in tropical countries.

15. Order **Zoraptera**. Pl. 1, V (C, D). This Order is erected for the genus *Zorotypus*, the systematic position of which is uncertain. These are small, carnivorous, tropical insects, living in the soil. The females are winged and have eyes; the males are often wingless and blind. The antennae are moniliform, the tarsi have two segments, and there are no visible genitalia.

Superorder ORTHOPTEROIDEA

The tarsi of this group have only three or four segments. The main difference between the Orthopteroidea and the Blattopteroidea lies in the method of oviposition. The Orthopteroidea (with the exception of the Plecoptera) have a specialized genital armature in the female, consisting of valves (gonapophyses) combined into an ovipositor.

16. †Order **Protorthoptera**. This Order was erected to receive a number

of Carboniferous and Permian forms, since extinct, which resemble the Protoblattids, but with the wing-venation simplified by reduction.

17. Order **Plecoptera**. Pl. 1, VII (9). Insects with aquatic larvae, commonly known as 'stone-flies'. The adult folds its wings backwards when at rest, and the abdomen ends in two long, multi-segmented cerci. Head prognathous, and with three ocelli. The larvae cling to stones in running water, and breathes by means of tracheal gills. There are 700 known species in the family PERLIDAE.

18. Order **Notoptera**. Pl. 1, V (E). The GRYLLOBLATTIDAE are wingless insects, elongate, orthognathous, with 5-segmented tarsi and multi-articulated cerci, and therefore primitive. Female with an ovipositor. These insects have cerci like those of the BLATTIDAE, but an ovipositor like that of the TETTIGONIIDAE. They are found in Japan (*Ishiana*) and at high altitudes in the Rocky Mountains (*Grylloblatta*).

19. Order **Cheleutoptera**. Pl. 1, VIII (3, 4). Insects that are often of very large size, and which may resemble leaves or twigs. Head more or less prognathous; wings often reduced, or even absent. Hind-legs not specialized for jumping. No stridulatory organs. Females with only a rudimentary ovipositor.

PHASMIDAE (*Bacillus*, *Phasma*, *Carausius*) imitate sticks of dead wood, and sometimes reach a length of 25–30 cm. PHYLLIIDAE (*Phyllium*) are well known because they look like walking leaves; their eggs are seed-like. Some species are parthenogenetic, and some (like *Carausius morosus*) have become laboratory animals, reared artificially, and used for a great many research purposes.

20. Order **Orthoptera**. Pl. 1, VIII (5, 6, 7). The Orthoptera, properly so-called, have the hind-legs elongate and specialized for jumping; in addition they have an auditory tympanum on the tibia. The mouth is always inclined ventrally (orthognathous), while it has been prognathous in all the previous groups. Wings well developed, and almost always stridulatory apparatus present.

More than 10,000 species of Orthoptera are known, some plant-feeding and some carnivorous. They are distributed into three big sub-orders: Tettigonioidea and Grylloidea, with long and filiform antennae, constitute the Order Ensifera on the one hand; on the other are the Acridioidea, with short antennae. This group includes the migratory locusts, which do immense damage almost everywhere in the tropics and sub-tropics.

21. Order **Embioptera**. Pl. 1, V (F). Small elongate insects with a big, prognathous head. The males have wings, but the females are apterous. Antennae filiform. Eyes well developed, but no ocelli. Fore-legs with the first tarsal segment swollen, and bearing silk-glands.

About seventy species are known, mostly tropical, in the one family

EMBIIDAE. These insects live under stones, in silken tunnels which they weave, and in which the female lays her eggs.

Superorder DERMAPTEROIDEA

Fore-wings completely converted into elytra, as in the beetles, hind-wings highly evolved, with a neala greatly extended, and folding like a fan underneath the elytra.

22. †Order **Protelytroptera**. This extinct Order flourished in the Permian of Texas, and had long elytra. The Protocoleoptera of the late Permian beds of Australia are related to these.

23. Order **Dermaptera**. Pl. 1, V (G, H, I). Tarsi three-segmented. Abdomen with cerci, which in the advanced forms have evolved into pincers (earwigs). Females without ovipositor.

Three sub-orders are recognized. The Forficuloidea are world-wide and are divided into several families, and the Arixenoidea are related parasitic and wingless forms (*Arixenia* is an Indian parasite of bats). The third sub-order, Diploglossata, is less closely related to the Forficuloidea, and includes *Hemimerus*, strange wingless insects which live in the fur of the Giant Rat (*Cricetomys gambianus*) in tropical Africa.

C. SECTION OLIGONEOPTERA

These are still Neoptera, but have the jugal field of the wing highly evolved, with the venation simplified down to a single vein that is never branched (*vena arcuata*). This section includes all the Holometabola (i.e. insects with a complete metamorphosis, and an immobile pupal stage). The Malpighian tubules are highly specialized in structure, but reduced in number to 2–6 (Oligonephridia), except in the Hymenoptera, where they remain very numerous.

Superorder COLEOPTEROIDEA

24. Order **Coleoptera**. Pl. 1, IX (1). Very variable in size, characterized by the possession of elytra, developed from the fore-wings. Except in *Melöe*, the elytra meet in the middle line, without overlapping. Head more or less prognathous, with mouthparts of the chewing type. Prothorax freely articulated with the rest of the body. The first sternite, and the tenth segment of the abdomen are always atrophied, so that the abdomen has only nine segments. Larvae generally with urogomphae on the ninth segment.

Most of the species are terrestrial, but there are also aquatic forms. More than 300,000 species have been described, and this number may be no more than a third of those existing in the world. There are 187 families. The first beetles appeared in the Permian.

Coleoptera are divided into four sub-orders:

Heterogastra and *Haplogastra* bring together a multitude of families that are diverse in appearance, but which have certain characters in common. The gonads are of a particular type, and the larvae have legs with only five segments, without the medius.

Adephaga (Caraboidea) lie on a totally different line, with quite a different structure of prothorax, abdomen and gonads, and with six-segmented legs in the larvae.

Finally, the *Archostemata* (*Cupes*, *Omma*) are a very old group, dating back to the Permian, and persisting to the present day, with a mixture of archaic and ultra-modern characters. CUPEDIDAE are few in number, and tropical. Pl. 1, XII.

Superorder NEUROPTEROIDEA

These are typical Holometabola, with two pairs of membranous wings; which have a large number of veins; many veins are bifurcate towards the margin, forming a fringe-like pattern round the wing. The mouthparts are of the chewing type; tarsi five-segmented; antennae almost always multi-segmented. These insects very numerous and very varied in the Permian and the Mesozoic.

25. Order **Megaloptera**. Pl. 1, IX (2). Very large, terrestrial insects, with aquatic larvae. Head prognathous; pronotum short; wings without pterostigma. The aquatic larvae are carnivorous, and have segmental abdominal legs, which function as gills. There are few of these insects, which fall into two families: CORYDALIDAE, with enlarged mandibles, and SIALIDAE.

26. Order **Raphidioptera**. Pl. 1, IX (3). Middle-sized insects, carnivorous, and terrestrial both as adults and as larvae. Head prognathous, like the preceding group, but the prothorax is always greatly elongate. Wings with a pterostigma. Very few in number, with a single family RHAPHIDIIDAE.

27. Order **Planipennia**. Pl. 1, IX (4-7). Very different from the foregoing in many ways. Head orthognathous; prothorax of normal proportions; wings very long. The carnivorous larvae are of very characteristic structure: mandibles long, and with a sucking channel; thoracic legs long; no abdominal legs, but an anal pygopod. Some of the larvae secrete silk in their Malpighian tubules, and pass it out through the anus.

This Order includes the HEMEROBIIDAE (*Chrysopa*, *Hemerobius*), the MANTISPIDAE, which have grasping fore-legs like the mantids, the NEMOPTERIDAE, in which the hind-wings are in the form of very long fringed plates, and lastly the MYRMELEONIDAE, the adults of which look like dragonflies, and whose larvae are known as ant-lions (*Myrmeleon*, *Ascalaphus*). Pl. 1, XI.

Superorder MECOPTEROIDEA

This Superorder, also called Petanoptera (Lameere) or the Panorpoïd Complex (Tillyard), centres round the Mecoptera, and includes on the one hand the Trichoptera and Lepidoptera, and on the other the Diptera. This association is based upon palaeontological evidence, because in the Trias of Australia we can find other Mecopterous insects which provide a link either with the Trichoptera or with the Diptera.

28. Order **Mecoptera**. Pl. 1, X (1). This Order flourished in the Permian and Trias of the southern hemisphere, but at the present time only relict groups are left. There are two pairs of membranous wings, without pterostigma, and the veins are simple at their tips (though there are a number of forks and cross-veins). The head is drawn out into a long beak, the mouthparts tending towards the licking and sucking type. Pl. 1, II (E). Antennae multi-segmented. Thorax very primitive, little sclerotized; tarsi with five segments. Larvae terrestrial, resembling caterpillars and having pseudopods. The two existing families are the PANORPIDAE and the BITTACIDAE.

29. Order **Trichoptera**. Pl. 1, X (2). Insects with aquatic larvae; head orthognathous, with mouthparts of the licking and sucking type; multi-segmented antennae; wings hairy, folded backwards and held roof-like when at rest; tarsi five-segmented.

The larvae are phytophagous, only rarely carnivorous, and almost all are aquatic, with tracheal gills on the abdominal sternities. Many of them live in cases, which they build themselves, but some weave a fabric over submerged stones, secreting the silk for this purpose with their labial glands. There are about 2,000 species, distributed among several families of these caddis-flies, as they are commonly called.

30. Order **Lepidoptera**. Pl. 1, X (3). Terrestrial insects, with the mouthparts modified into a coiled proboscis. Pl. 1, II (D). Antennae of variable structure. Prothorax always reduced, most often equipped with patagia. Wings large, covered with scales, usually folded backwards, roof-like when at rest, but occasionally held out horizontally (Rhopalocera). Tarsi five-segmented.

Adult Lepidoptera feed on nectar and pollen; their larvae (caterpillars) are phytophagous, or only rarely zoophagous. Pupae obtect (chrysalides), very often enclosed in a cocoon.

More than 100,000 species of Lepidoptera are known, grouped into two sub-orders, which are distinguished by the way in which they link the fore-wing to the hind-wing, with a coupling apparatus. *Jugata* are the more primitive (MICROPTERYGIDAE, HEPIALIDAE), and are related to the Trichoptera; *Micropteryx* still retains mandibles. *Frenata* are by far the bigger group, and include a large number of families.

The old classification of Lepidoptera into Heterocera (with filiform or

PLATE 1 – IX. PTERYGOTE INSECTS (OLIGONEOPTERA)

ORDER COLEOPTERA

1. *Melolontha vulgaris* (Scarabeidae).

ORDER MEGALOPTERA

2. *Sialis lutaria* (Sialidae).

ORDER RAPHDIOPTERA

3. *Raphidia notata* (Raphidiidae).

ORDER PLANIPENNIA

4. *Chrysopa vulgaris* (Chrysopidae).
5. *Mantispa pagana* (Mantispidae).
6. *Formicaleo tetragrammicus* (Myrmeleonidae).
7. *Nemoptera sinuata* (Nemopteridae).

IX



X



PLATE 1 – X. PTERYGOTE INSECTS (OLIGONEOPTERA)

ORDER MECOPTERA

1. ***Panorpa communis*** (Panorpidae).

ORDER TRICHOPTERA

2. ***Rhyacophila vulgaris*** (Rhyacophilidae).

ORDER LEPIDOPTERA

3. ***Papilio machaon*** (Papilionidae).

ORDER DIPTERA

4. ***Volucella zonaria*** (Syrphidae).
5. ***Lucilia sericata*** (Calliphoridae).
6. ***Bombylius major*** (Bombyliidae).

ORDER HYMENOPTERA

7. ***Discolia hirta*** (Scoliidae).
8. ***Xylocopa violacea*** (Apidae).
9. ***Anoplius viaticus*** (Pompilidae).

pectinate antennae) and Rhopalocera (with clubbed antennae) has been given up, and at the present time the families are classified according to the wing-venation.

31. Order **Diptera**. Pl. 1, X (4, 5, 6). Insects with only a single pair of wings, the hind pair being transformed into balancing organs (*halteres*). Mouthparts of a piercing and sucking type; mandibles and maxillae converted into piercing stylets, but often the reduction of the stylets is correlated with a change to sucking habits. Tarsi five-segmented. Antennae multi-segmented in some (Nematocera); reduced to a shorter type, with arista, in the rest (Brachycera). Larvae legless, with the head little or not at all developed; some terrestrial, others aquatic. Feeding-habits most diverse.

More than 50,000 Diptera have been described, in four sub-orders: Nematocera; Brachycera (Orthorrhapha); Cyclorrhapha, Pupipara. The last of these (including HIPPOBOSCIDAE and NYCTERIBIIDAE) are parasitic.

Superorder SIPHONAPTEROIDEA

32. Order **Siphonaptera**. Pl. 1, VI (A). These are the fleas, and were formerly called *Aphaniptera*. They have to be put in a Superorder of their own because we do not know what their real affinities are. Some have wanted to put them close to the Coleoptera, on account of their larvae, but the general opinion is that they belong near the Diptera.

They are sucking insects, all wingless parasites. The integument is tough, and covered with spines, all of which are directed backwards, and often arranged in combs (*ctenidia*). Antennae with scape and pedicel well developed, but flagellum fused into a single unit. Larvae wingless, but with a specialized head. Only the adult is parasitic on mammals and birds; the larva is free-living, feeding on debris and spores of fungi or moulds. There are a number of families and a great many species.

Superorder HYMENOPTEROIDEA

33. Order **Hymenoptera**. Pl. 1, X (7, 8, 9). Insects with four wings; head orthognathus: mouthparts chewing or licking and sucking; mandibles always developed; no gula; almost always three ocelli on frons. The first segment of the abdomen is fused with the metathorax, forming a unit known as the 'mediary segment' or *propodeum*. Tarsi five-segmented, with a bilobed arolium. The females have an ovipositor of the same type as that of the Orthoptera. Larvae most often legless.

The origin of the Hymenoptera is unknown, but they first appear as fossils in the Jurassic period. They are nearly all terrestrial, though *Prestwichia* (CHALCIDIDAE) is aquatic, and swims by means of its wings. In the adult state they are either carnivorous, or feed on pollen or honey; the larvae are phytophagous or carnivorous, and many are parasites. The

behaviour of the different groups varies widely. Wasps are predatory, and supply their larvae with paralysed food to eat; many bees are social.

About 100,000 species are known, but the tiny parasitic forms (CHALCIDIDAE, PROCTOTRUPIDAE, CYNIPIDAE) have been very incompletely studied, and many must be still unknown. It is possible that several hundred thousand Hymenoptera really exist.

Hymenoptera are divided into several sub-orders. *Symphyta* have the abdomen sessile at the base, without a 'waist'; these are the phytophagous sawflies (Tenthredinoidea). In the *Terebrantia* the females have a long auger-like ovipositor, and larvae which are endoparasitic on other insects (ICHNEUMONIDAE, CYNIPIDAE, CHALCIDIDAE, PROCTOTRUPIDAE). The *Aculeata*, a third sub-order, includes CHRYSIDIDAE, MUTILLIDAE, and the ants, bees and wasps.

34. Order **Strepsiptera**. Pl. 1, VI (B). Very small, parasitic insects. The males have wings, the hind pair being folded and fan-like, while the fore pair are modified into balancers (*halteres*); the antennae are flabellate (with blades like a closed fan). The males live only a few hours, and do not feed, their alimentary canal being closed. The adult females, and the larvae of both sexes, are endoparasitic.

Strepsiptera were long considered as degenerate Coleoptera, but on the contrary they are related to Hymenoptera. About 200 species are known, grouped into several families. MENGEIDAE (*Eoxenos*) are parasites of Thysanura (*Lepisma*). STYLOPIDAE attack Hymenoptera, Homoptera and Orthoptera. A wasp that has been parasitized, generally a female, is said to be 'stylopized'; the effect of such parasitism is to destroy the female characters and make the insect more like a male (parasitic castration).

D. SECTION PARANEOPTERA

This third section of the Neoptera has the jugal field of the wing as highly evolved as in the Oligoneoptera, with only a single vein remaining, though this is branched at the tip. Like the Oligoneoptera, the Paraneoptera are oligonephridian; but like the Polyneoptera they are hemimetabolous. The tarsi never have more than three segments.

Superorder PSOCOPTEROIDEA

35. Order **Psocoptera**. Pl. 1, VI (C). These are also known as Copeognatha, Corrodentia, or Psocids. They are tiny insects, short-bodied, with a huge prognathous head, chewing mouthparts and globular abdomen. Antennae long and multi-segmented. Tarsi with two or three segments. Wings often absent. About 800 species, most abundant in warm countries. Predominantly 'microphagous', feeding on spores, moulds and fragments of organic debris.

36. Order **Mallophaga**. Pl. 1, VI (D). Small, flattened insects, ectoparasites of birds and mammals. They live on debris from the skin of the host, hairs and feathers. Head broad and depressed, with five-segmented antennae. The mouth is ventral, and has chewing mouthparts. Tarsi of one or two segments; no wings. About 1,500 species are known, most of them from birds.

37. Order **Anoplura**. Pl. 1, VI (E). While the Mallophaga and the Psocoptera are clearly allied, the position of the Anoplura is less certain, and they are placed here with reservations. Lice are biting insects, with a prognathous head, and highly evolved mouthparts. Eyes are simple if present, but are often absent. Antennae short, with numerous segments. No wings. About 150 species are known, in several families, and all are ectoparasites.

Superorder THYSANOPTEROIDEA

38. Order **Thysanoptera**. Pl. 1, VI (F). The 'thrips', or 'Physopoda', are very small, elongate, and all terrestrial. Head hypognathous, the mouthparts of a sucking type, and asymmetrical. Antennae standing close together on the frons. Tarsi with two segments. Wings narrow, fringed with long hairs.

About 1,000 species, some carnivorous, some phytophagous. The phytophagous forms are often extremely harmful to fruits and other cultivated plants. The *Terebrantia* have antennae with 6–10 segments, and the fore-wings stiffer than the hind ones. The *Tubulifera* differ in the structure of the proboscis, and have eight-segmented antennae, and all four wings alike.

Superorder HEMIPTEROIDEA

Very variable in size, but characterized by their special type of proboscis, as in Pl. 1, II (F). Fore-wings always different from the hind-wings.

39. Order **Homoptera**. Pl. 1, VI (G). Terrestrial insects. Fore-wings entirely membranous; hind-wings much shorter than the fore pair. Metathorax reduced.

All Homoptera feed on plants, and nearly 20,000 species are known, mostly from warm countries. They are grouped into several sub-orders, arranged in two series: Sternorrhyncha and Auchenorrhyncha. These had diverged by the Permian from a primitive group, Palaeorrhyncha, found in Australia.

Sternorrhyncha have long antennae, and their proboscis (rostrum), which is directed backwards, seems to arise between the fore coxae (Hypognatha). Tarsi with one or two segments. Many of this group,



Plate 1 - XI *Ascalaphus libelluloides* (Order Planipennia)



Plate 1 - XII *Cupes raffrayi* from Madagascar (Order Coleoptera)

especially among the females, are unable to move, and remain fixed in one spot (COCCIDAE; PSYLLIDAE, plant-lice).

Auchenorrhyncha have very short antennae, ending in a bristle. Head orthognathous. Tarsi three-segmented. Here we have the Cicadas, CERCOPIDAE, JASSIDAE and FULGORIDAE, all very numerous on vegetation throughout the world. Most of them are capable of jumping.

40. Order **Heteroptera**. Pl. 1, VI (H, I). Either terrestrial or aquatic insects. The first pair of wings is transformed into 'hemelytra'; i.e. the basal part is leathery (*corium*), and the apical part membranous. Scutellum always big. Tarsi always three-segmented.

About 25,000 species are described, from all over the world, some groups being phytophagous, some predatory. The first Heteroptera appeared in the Trias of Australia. Living forms are grouped into two sub-orders.

The *Gymnocerata* comprise mainly terrestrial forms (PENTATOMIDAE, CAPSIDAE, LYGAEIDAE, REDUVIIDAE, CIMICIDAE, COREIDAE, etc.), and also some which live on the surface of water (*Velia*, *Gerris*, *Hydrometra*). The *Cryptocerata*, on the other hand, are all aquatic, and adapted to swimming in the water. These are the true water-bugs, and are all carnivorous (NAUCORIDAE, BELOSTOMIDAE, NEPIDAE, NOTONECTIDAE, etc.).

Part Two

BIOLOGY

6

Physiology

NUTRITION

Feeding habits. Endoparasitic species, such as the Strepsiptera, which live immersed in the tissues of their host, and feed by osmosis through the integument, may have no alimentary canal. Apart from these, the great majority of insects have a functional alimentary canal, which is often very complex, and they can be grouped into various categories, according to their feeding habits. It is customary to divide them into phytophagous, carnivorous and omnivorous forms.

In practice, the admission of a category of omnivorous forms serves only to underline the fact that there is no clear line of division between those which are phytophagous and those which are carnivorous. Many insects are not specialized in their feeding habits, and will accept a wide variety of food material. It would be better to call these forms *polyphagous*, in contrast to those *monophagous* insects which confine themselves to one particular species of plant or animal.

Furthermore, we must distinguish between those insects which devour



Fig. 57 – A phytophagous bug,
Graphosoma italicum
(Pentatomidae), from France.

living animals or plants, and those which merely absorb nutriment from organic matter that is already dead and decomposing. These latter are said to be *saprophagous*.

Very many saprophagous insects feed upon organic matter of vegetable origin that has accumulated on the ground.

Looking at it from another point of view, we can say that many insects take solid food, which they have to chew, while a comparable number take liquid food, either directly, or by piercing the tissues of animals or plants to get at the internal fluids. These differences in feeding habits are accompanied by modifications of the mouthparts, as we have seen in the first section of this work, and by correlated differences in physiology.

To divide the insects into the three categories of carnivorous, phytophagous and saprophagous forms does not go far enough, and within each of these we have to recognize further subdivisions.



Fig. 58 – A wood-feeding weevil; *Heteromus quadricollis* (after FLEUTIAUX). On the right, the adult emerging from its puparium, made from wood-fibres twisted together.

A *phytophagous* form in the strict sense browses on green plants, and sucks their juices by means of a proboscis (Fig. 57). It may be a leaf-feeder, a flower-feeder or a root-feeder, or it may be a gall-forming species, sheltering and feeding inside a vegetative outgrowth (gall) which the plant forms in response to the irritation of the feeding of the insect.

Xylophagous insects eat wood (Fig. 58). The majority can assimilate only starchy and sugary substances in the sap-wood, but a few, including larvae of certain Cerambycid and Anobiid beetles, are able to break down cellulose into glucose. Generally speaking, insects themselves cannot make the diastases which can digest cellulose: it has been shown that certain termites have this done for them by Protozoa living in the gut of the insect, but in most cases the mechanism remains a mystery.

Clethrophagous insects are specialized to feeding in grain. Carabid beetles, normally carnivorous, may sometimes be adapted to grain-feeding, like the genera *Zabrus* and *Ditomus*, which collect the seeds of grasses and store them in burrows. Many CURCULIONIDAE and BRUCHIDAE are exclusively grain-feeders, and in consequence rank as major insect pests, because of their attacks on stored products.

Microphagous insects are usually very small ones, which live on minute

particles of food. Some feed on grains of pollen, and many that are found in vegetable debris, and are generally considered to be saprophagous, actually live on yeasts, bacteria, or microscopic spores, that is on living organisms. *Mycetophagous* insects are plant-feeders of a special kind, living only on fungi, and often very exclusive in their habits. Beetles of the family LIODIDAE (*Bolboceras*) seek out subterranean fungi and break them up by excavating deep tunnels.

Carnivorous insects, whether they bite and chew or pierce and suck, are often highly specialized. *Predators* pursue living prey (Fig. 59). Most of them attack smaller animals (worms, molluscs, insect-larvae) and are not particular in their choice, but many confine themselves to one kind of prey or even to one species. All gradations exist between the general predator and the specific parasite. *Necrophagous* insects come only to dead animals. Some seek rotting flesh, some fat, dried and mummified tissues, hairs or feathers (*Trox*), and as a result of these specialized tastes corpses of the larger animals are visited by a succession of different groups of insects. Some avoid the bigger corpses and come only to small ones, such as those of insects.

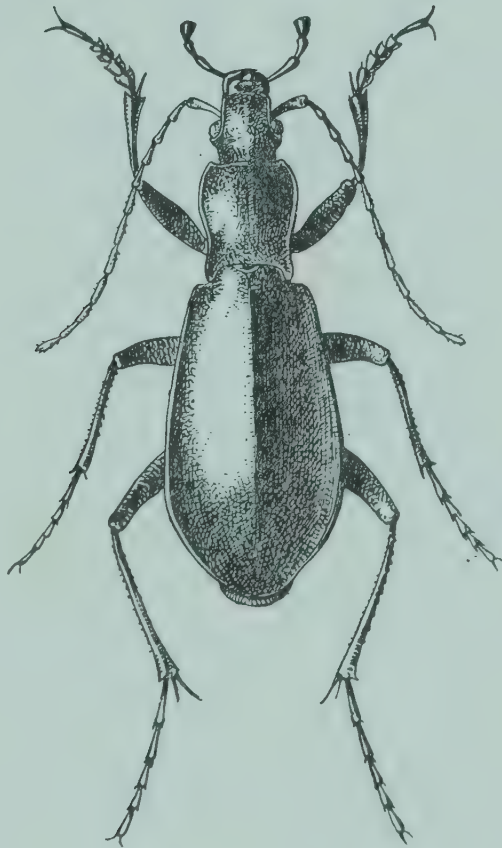


Fig. 59 – A carnivorous beetle, *Carabus splendens* (Carabidae), from the Pyrenees.

Coprophagous insects make use of animal excreta (Fig. 60), and here again there are specialized habits. Obviously the great host of coprophagous insects that follow ruminants and equines feed largely on matter of

vegetable origin. On the other hand certain mammals provide a specialized diet for coprophagous insects: e.g. the bats, whose dung crawls with guano-feeding insects.

Digestion. The digestive juices are produced by the salivary glands and from the mid-gut. The saliva has several functions. Sometimes it is no



Fig. 60 – A dung-feeding Lamellicorn, *Ateuchus sacer* (Scarabeidae), from the Midi of France.

more than a solvent for solid sugars, which are more easily taken in in liquid form (Lepidoptera), but more often there is chemical action as well. The saliva of bloodsucking flies contains an anticoagulant; that of Homoptera is injected by means of a double-action pump (Fig. 61) and serves to attack and break down plant-cells. Again, in many insects, the saliva contains digestive enzymes, amylases and diastases, which transform the food material into compounds which can be assimilated.

In bees, where the saliva is required to do a number of different things, glands have been found to open on the mandibles, the labium and the pharynx. The last produce diastase, and are particularly active in making ‘royal jelly’, which feeds the first-stage larvae and larval queens.

The digestive juices produced in the mid-gut vary greatly according to the feeding habits of the insects concerned. Omnivorous insects have the greatest variety of secretions, while monophagous insects tend to have simpler digestive secretions. Carnivores have enzymes suited to the digestion of proteins and fats; phytophagous insects those enzymes suited to the carbohydrates.

We have already mentioned that the larvae of certain wood-boring beetles (Cerambycids, Anobiids) can digest cellulose directly: in a similar way larvae of *Lucilia* (Diptera) have collagenase, which dissolves connective tissue, and larvae of *Galleria* (Lepidoptera) can digest wax.

Dermestid beetles, and Mallophaga, can assimilate the keratin of hairs and feathers; Microlepidoptera and the beetle *Anthrenus* digest silk. Many insects whose pupal stage is passed in a silken cocoon have digestive enzymes capable of softening silk and thus helping the adult to break out from the cocoon.

Extra-oral digestion. Many carnivorous insects inject saliva into their prey, and feed only upon substances that have been liquefied and partly digested in this way. This method of pre-digestion is standard in biting insects (e.g. mosquitoes), and has been observed in some beetles, mainly in larvae. It has even been supposed that wood-boring beetles may excavate their galleries more by dissolving the wood with their saliva than by chewing it with their mandibles.

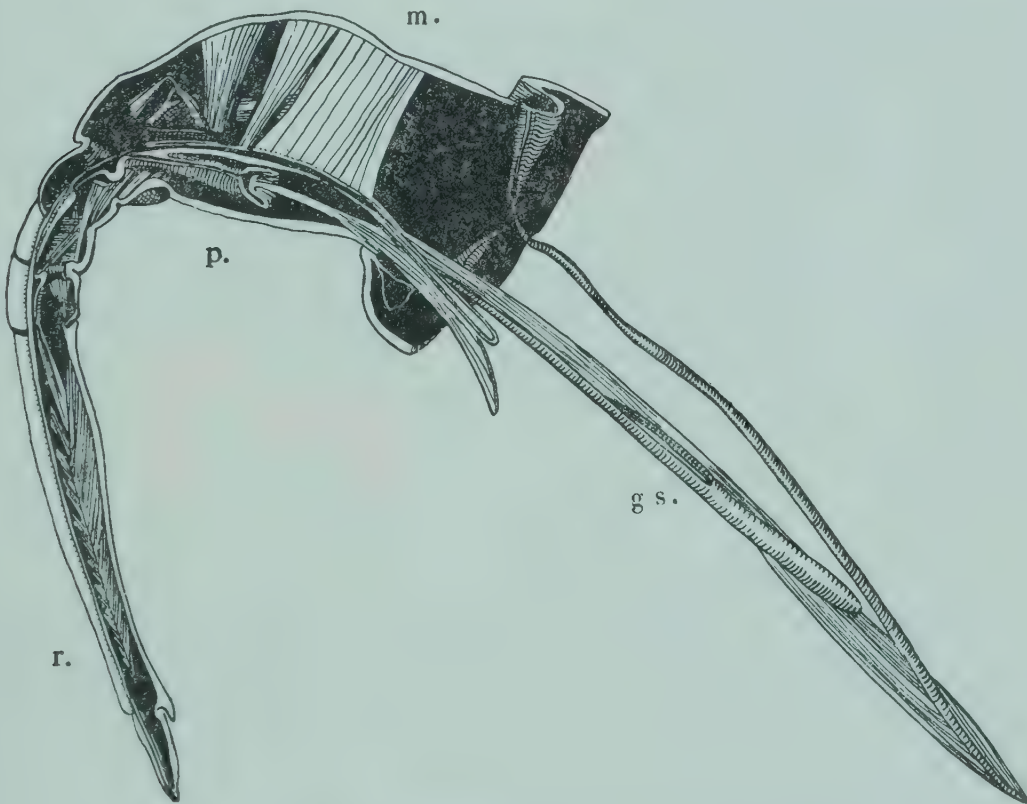


Fig. 61 – Longitudinal section of the head of a Gerrid bug. (after WEBER). m, retractor muscles of the pharynx; g.s., salivary glands; p, salivary pump, with both suction and forcing actions; r, rostrum.

Those SILPHIDAE that feed on snails pour out a great deal of saliva containing proteolytic enzymes to liquefy their prey before ingesting it. The larvae of LAMPYRIDAE (fireflies) and of DYTISCIDAE have perfected this way of feeding. The mandibles of Lampyrid larvae (Fig. 62) have a longitudinal groove along which the saliva flows. When such a larva has inserted its mandibles into the body of a snail it shakes its head violently to help the flow of saliva, which first paralyses the snail, and then dissolves

its tissues. When the snail quickly retracts into its shell, it carries with it the Lampyrid larva, which remains clamped on to its prey and does not let go until it has absorbed all the pre-digested food that is available.

The stages of this process of pre-digestion are easily watched in the larvae of *Dytiscus* in an aquarium, because these larvae are transparent. The injection of a colourless toxic saliva can easily be seen, followed by a coloured secretion from the intestine. The partly digested material is then sucked in, and injection and suction follow each other until the prey is totally drained of its fluids.

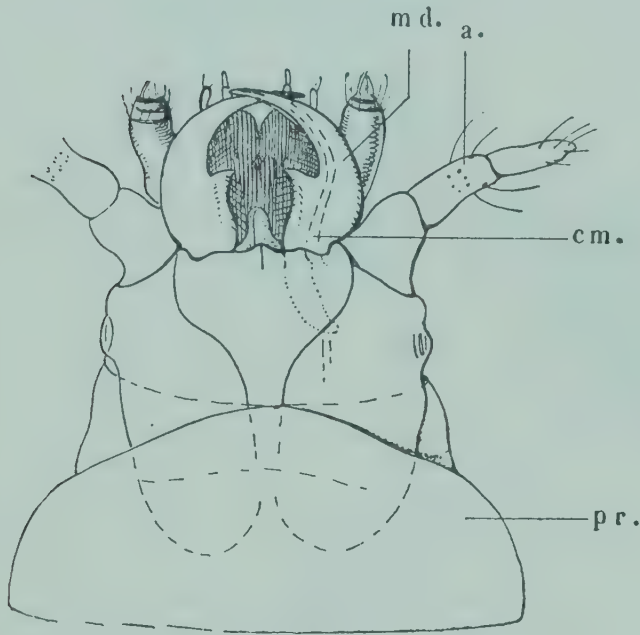


Fig. 62 – Head of the larva of *Lampyris noctiluca*, showing the mandibular canal (dotted) (after VOGEL). m.d., mandible; c.m., mandibular canal; a, antenna; pr, prothorax.

Intestinal digestion. Whether it has been pre-digested or not, the food passes through the *oesophagus*, and accumulates in the *crop*. From there it passes to the *proventriculus*, or gizzard, where it is mixed together and ground down into a finely divided state, before passing through the *cardiac valve* into the mid-gut.

In the mid-gut the pellet of food is enclosed in a sort of chitinous tube secreted by the ectodermal cells in the region of the cardiac valve. This *peritrophic membrane* is very fine, and is permeable to both the digestive enzymes and the absorption products of the food. It keeps the food out of direct contact with the delicate epithelial cells. The membrane is formed continuously, and the cylinder of chitin thus formed is drawn into the hind-gut by peristalsis, and evacuated through the anus. When the insect is young the peritrophic membrane passes out empty, but later on it is packed tight with the waste products of digestion.

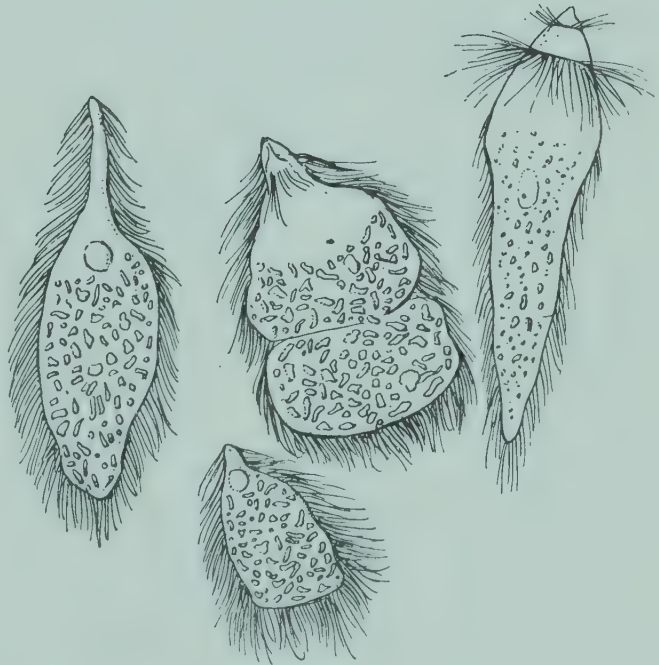
The *rectum* is most often a large reservoir, and plays an important part in the digestive process. In the first place there are rectal glands, whose

exact function is uncertain, but which are believed to absorb water from the faecal pellet. Then, many insects (termites, Tenebrionid and Scarabeid beetles, for example) have flagellate Protozoa living in the rectum (Fig. 63). The function of these Protozoa is debatable. Those Coleoptera that harbour them are mostly phytophagous, and therefore pass into the intestine great quantities of cellulose. As far as the termites are concerned, there is more evidence of the part played by the Trichonymphite flagellates in the rectum. These have been shown to be essential in the digestion of wood, and in making the faecal food that is so important in the biology of the termite colony. Deprived of their Trichonymphs, the termites die of malnutrition.

Termites are far from being the only insects to manufacture a faecal food. The excreta of Aphids contain sugary matter that is eagerly eaten by ants. The faeces of insects also serve a number of other purposes. Many larvae use faecal material as a shelter for pupation, and others such as the Cassid and some Chrysomelid beetles (*Criocera*) have the anus directed dorsally, so that excreta accumulate and form a sort of protective carapace for the body.

Mycetomes. It was discovered not very long ago that there are special assemblages of micro-organisms (bacteria) which occur sometimes among the cells of the alimentary canal, or in the vicinity, and sometimes in the

Fig. 63 - Trichonymphs (Flagellate Protozoa) from the hind-gut of Mesotermitidae (after HEGH).



genital ducts. These are known as *mycetomes* (Fig. 64). Collectively they fulfil a special function, and are often found to be packed with bacteria, which have been extracted and cultivated by standard bacteriological methods. On the other hand they may not always have bacteria; e.g.,

those of the Curculionid beetle *Sitophilus oryzae* have them, but the mycetomes of *Sitophilus granarius* are sterile.

Mycetomes may be sited in any of the various regions of the mid-gut, or hind-gut, and several categories have been recognized. Some are directly linked with the Malpighian tubules, or again with the wall of the gut, while others are entirely cut off from the alimentary canal (BOSTRYCHIDAE, LYCTIDAE).

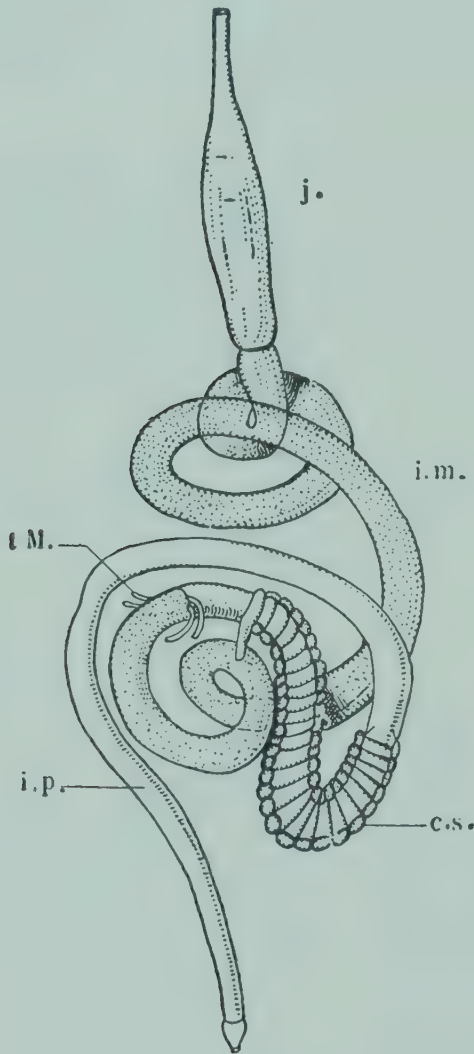


Fig. 64 – Alimentary canal of *Popilius disjunctus* (a Passalid beetle) (after LEWIS). j, crop; i. m., mid-gut; t.M., Malpighian tubules (cut off short); i.p., hind-gut; c.s., mycetomes (cells full of symbionts).

It is chiefly the xylophagous insects, or those which feed on keratin, or wax, or other substances difficult to digest, that have mycetomes, but they may occur sometimes in carnivorous insects. It seems likely that where mycetomes occur in close association with the alimentary canal they are helping in the digestion of cellulose, but this has never been conclusively proved.

On the other hand we can say definitely that these micro-organisms are transmitted from one generation to another by way of the egg, and that this operation is an essential part of the development of the insects.

Consequently there is a growing tendency to infer that mycetomes are necessary for proper growth, and no doubt they manufacture something of the nature of vitamins, the role of which in insect physiology is only now beginning to be suspected.

Metabolism. Digestion produces three kinds of substance that can be assimilated by the body: fats, carbohydrates and proteins.

Fats build up in the fat body during larval life, and constitute the main source of energy for metamorphosis.

Carbohydrates are held in reserve in the fat body, but in addition they enter into the composition of the blood and of most tissues. They are the main source of energy for the adult insect. It has been estimated that a bee in flight, weighing 100 mgm., will consume about 10 mgm. of sugar per hour. In fifteen minutes' flight the bee will cover $5\frac{1}{2}$ km., and will then have exhausted its normal stock of carbohydrates, and be incapable of further flight. It gets the necessary kind of food from nectar and honey.

Finally, proteins are used to repair the muscles and other tissues, and are vital to the maturation of the gonads.

Water is essential to insects, as can be seen by studying the dispersion of insects into different types of habitat. The proportion of water in the insect's body varies from 50 to 90 per cent. Water is lost by evaporation, either through porous membranes, or through the spiracles, and may be replaced orally (for many insects drink), or by the water that is produced during the chemical reactions of metabolism.

EXCRETION

The elimination of waste-products that accumulate in the blood is brought about in insects by excretory organs of two principal sorts: the Malpighian tubules and the fat body.

The Malpighian tubules. We have seen that these vary both in number and in structure. They are ectodermal structures, opening at the beginning of the hind-gut, and number anything from 2 to 150 in different groups of insects, showing many modifications of structure. There is no doubt that they serve as kidneys, and filter out a urine bearing waste materials in solution. In the bug *Rhodnius* it has even been demonstrated that the distal part of the tubule is excretory in function, while the more proximal part is concerned primarily with reabsorption. In the caterpillars of Lepidoptera, and in the cryptonephridial Coleoptera, the way in which the Malpighian tubules have their distal ends attached to the wall of the rectum would seem to facilitate absorption of water by the rectum.

The urine excreted by the Malpighian tubules mixes with the solid waste in the hind-gut, giving faecal matter that is both fluid and abundant, indeed liquid in insects whose diet is fluid. Some of the watery content is

lost in the rectum. The composition of the faecal matter varies: it is acid or alkaline according to the diet, but always contains phosphates and sulphates, and above all nitrogenous products such as ammonia, urea, uric acid and amino-acids.

The excretion of nitrogenous products is not the only function of the Malpighian tubules. The urine of Coeloptera, Diptera and caterpillars of Lepidoptera contains also pigmented compounds, carbonates and oxalates, and calcium salts. One Australian Cercopid bug of the genus *Ptyelus* excretes through its Malpighian tubules enough calcium carbonate to

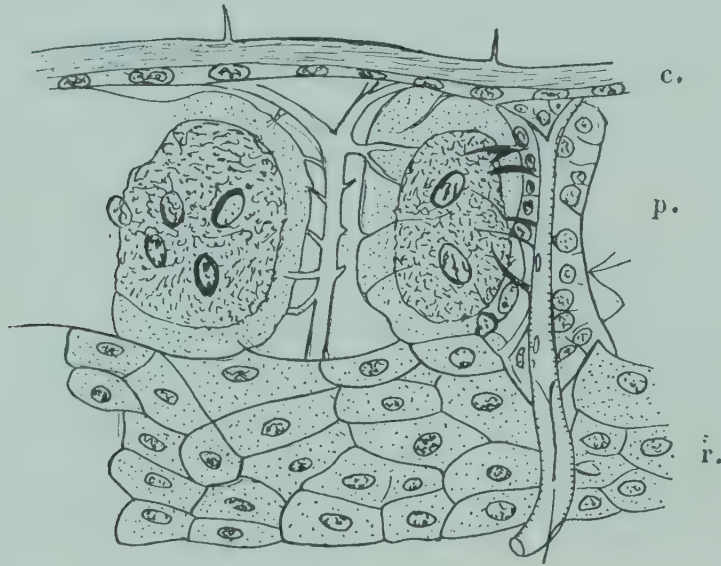


Fig. 65 – Section of a luminous organ of *Luciola* (after WILLIAMS). c, cuticle; p, light-producing organs, supplied with oxygen by tracheoles; r, reflecting layer, consisting of cells packed with crystals of urates and of xanthine.

build itself a spiral shell. The larvae of *Chrysopa* (Neuroptera) and those of *Lebia scapularis* (Carabid beetle) secrete silk in their Malpighian tubules, and pass it out through the anus in order to make a cocoon.

The fat body. The fat body of a larva is primarily a store of fats and glycogen, which accumulate in the cells, but certain cells also serve as a kidney, and eliminate nitrogen by storing solid urates. At the end of larval life these solid waste products are passed into the intestine during the pupal reorganization, and are voided among the first faeces of the adult insect. As we have seen, the fat body is in two parts, one round the intestine and one beneath the integument, and the latter is sometimes specialized into luminous organs.

Luminous organs. Apart from the luminosity produced by bacteria during decay, nearly all light-production in insects is confined to the Coleoptera, to Collembola whose whole body is luminescent, and to the

fly *Bolitophila luminosa*, which produces light at the tips of the four Malpighian tubules.

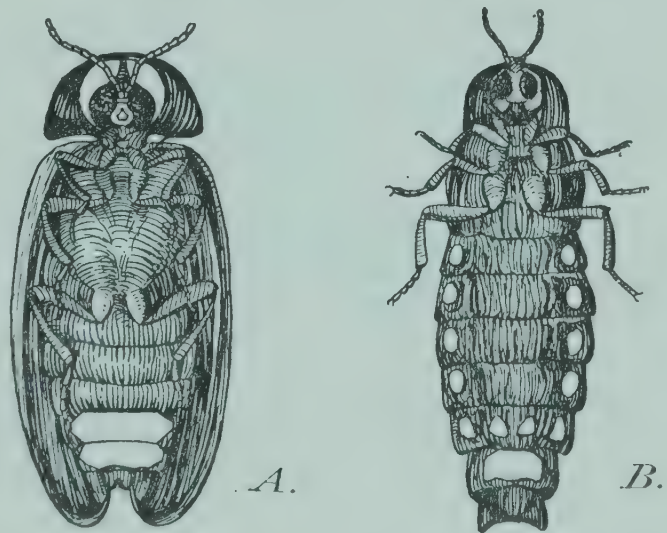
Among Coleoptera there is one Paussid, *Paussus sphaerocerus*, living in ant-hills in Dahomey, whose antennae appear as two great luminous spheres: otherwise all the luminous beetles belong to the two families LAMPYRIDAE and ELATERIDAE, the glow-worms and fireflies. The LAMPYRIDAE have their luminous organs on the abdomen, and the Elaterids on the sides of the thorax, only rarely with additional ones on the abdomen or the elytra.

These organs (Figs. 65 and 66) occur on the cuticle, and consist of two layers of cells derived from fat body: the upper layer is packed with globules of fat, and is well supplied with herves and tracheae; the lower is a reflecting layer of cells filled with crystals of urates and of xanthine. The upper layer is the photogenic one, where luciferin, of fatty origin, is oxydized in the presence of an enzyme (luciferase), to give an oxyluciferin, which is luminous. This reaction is under the control of the insect, and can be accelerated or retarded by varying the supply of air to the tracheoles.

The light thus produced is a 'cold light', with a very short spectrum, and with a luminous efficiency far greater than that of any man-made source of light. Nevertheless, it requires thirty-seven to thirty-eight fireflies to give one candle-power.

LAMPYRIDAE are luminous in all stages after the egg, but the light is principally used to bring the sexes together for mating. The colour of the

Fig. 66 - *Phausius splendidulus* (Lampyridae), male (A) and female (B), seen from the ventral side (after KUKENTHAL). Luminous organs shown in white.



light emitted varies from greenish to red. The genus *Phengodes* has luminous organs of two colours, red on the anterior part of the body and green on the abdomen.

Miscellaneous secretions. Many insects make silk, in a variety of

different ways. *Chrysopa* and some Carabid beetles make it in the Malpighian tubules; Lepidoptera, Hymenoptera and even some Orthoptera make it in labial glands; Hydrophilid beetles in accessory glands of the genital organs; Embioptera in glands in the anterior tarsi.

Some Hymenoptera (bees) and some Hemiptera (Fig. 67) secrete wax, which is composed of alcohols and fatty acids associated with paraffins. Similar compounds make the solid, coloured secretions in the integument of certain Curculionid beetles (*Larinus*, *Lixus*), and the secretions of the peristigmatic glands of the DYTISCIDAE. These waxy secretions produce

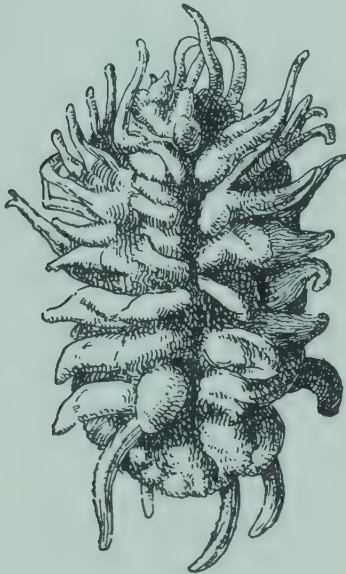


Fig. 67 – Larva of *Cryptolaemus montrouzieri* (Coleoptera), covered with a waxy secretion (after BERLESE).

hydrofuge areas in the bodies of aquatic insects, and in the terrestrial species they serve to restrict evaporation from the body-fluids. The lacs secreted by COCCIDAE (Homoptera) are other waxy products that are mixed with resins and a variety of pigments.

Many insects secrete venom, which they inject into their victim either by modified genitalia, as in the aculeate Hymenoptera, or by the proboscis, as in Heteroptera. Others have violent poisons in their blood. It is curious how the insects are able to secrete extremely toxic substances, either simple or complex, in a pure state. The pygidial glands of Carabid beetles secrete butyric acid; the caterpillars of *Notodonta concinnula* emit hydrochloric acid; those of *Dicranura vinula* (Fig. 68) harden their cocoon with 40 per cent formic acid; *Paussus* may have pure iodine in its tissues.

RESPIRATION

The mechanism of respiration in insects is quite different from that of vertebrates. In the latter the blood passes to the lungs, where it fixes oxygen by use of haemoglobin, and then carries it to the various organs. In insects the oxygen is led directly to the tissues by a network of tracheae,

without using any intermediate carrier. Haemoglobin does exist in the blood of larval CHIRONOMIDAE (Diptera), but the great majority of insects show no trace of anything of the kind; haemocyanin, which plays the part of haemoglobin in the blood of molluscs, has never been found in insects.

Transport of oxygen by the tracheae. Cutaneous respiration is common in aquatic insects, but exceptional in terrestrial ones. This must have been the original method of respiration in the ancestral group, tracheae being developed as invaginations from the ectoderm when the first insects began to take up life in a dry atmosphere. At the present time the only insects that still breathe through the cuticle are the aquatic ones, some cave-dwelling forms which live in an atmosphere saturated with moisture, and tiny forms such as Collembola, where the area of surface is great in proportion to the volume.

The air circulates in the tracheae, but exchange of oxygen and carbon dioxide does not take place everywhere along their length. Remy injected bleached indigo (which is colourless) into Ephemeroptera and Neuroptera, and noted where it turned blue, indicating that an exchange of oxygen was going on there. This occurred only in the tracheolar cells, which form a syncytium round each organ, and into which the minute branches of the

Fig. 68 – Caterpillar of *Dicranura vinula* (Lepidoptera; Notodontidae). This caterpillar secretes formic acid at the time of pupation.



tracheoles disappear. Neither the tracheal trunks, nor the air-sacs, nor yet even the tracheal gills of aquatic insects gave this reaction. It is clear, therefore, that intake of oxygen is possible only in the organs themselves, notably in the muscles, the fat body, and the Malpighian tubules. In the muscles the oxygen is held by certain organic substances (cytochrome, glutathione) which act as reservoirs, or accumulators.

To reach the tracheolar network, the air has to circulate a long way through the tracheal system. This is achieved by mechanical means, through abdominal movements, assisted by rhythmical opening and

closing of some of the spiracles. As a general rule, the anterior spiracles open to take in air, and the posterior ones to expel it, thus maintaining a current of air through the body from front to rear. It has been shown that this 'forced draught' is more powerful in insects (Fig. 69) than it is in man. A cockchafer was shown to expel one-third of the air contained in its tracheal system at each contraction, whereas a man expels only one-seventh.

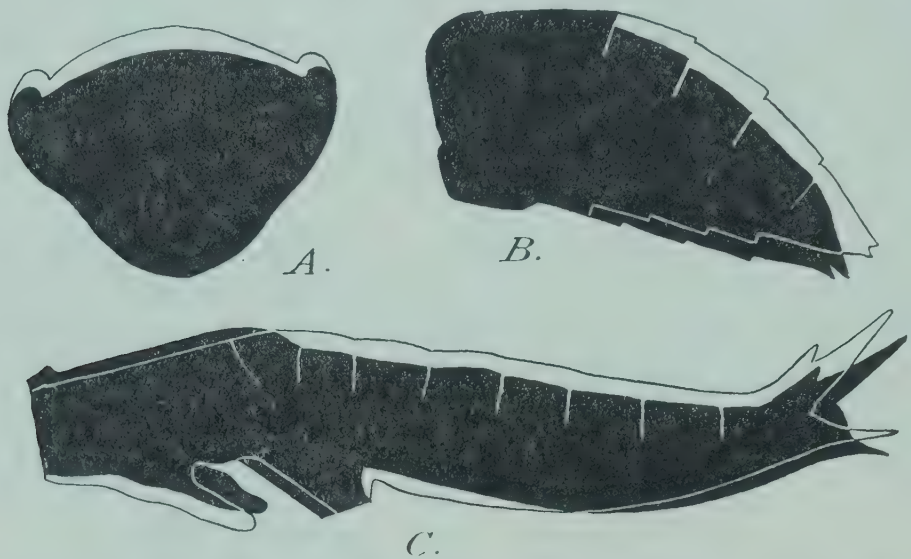


Fig. 69 – Diagram showing the respiratory movements of: A, *Oryctes nasicornis*; B, *Vespa germanica*; C, *Blatta orientalis* (after PLATEAU).

Carbon dioxide is only partly expelled through the tracheae. Most of it diffuses through the tissues and out through the integument, since it diffuses much more freely than oxygen. In particular, it escapes through the membranes of the abdomen.

As in vertebrates, the respiratory circulation is controlled by reflexes. Lack of oxygen in the air drawn in, or excess of carbon dioxide in the tissues, will produce a wider and longer reflex opening of the spiracles, and speed up the respiratory movements.

Aquatic insects. Aquatic insects have a great variety of respiratory



Fig. 70 – Larva of *Chironomus* (Diptera); apneustic type (after MIALL).

mechanisms, a fact which is consistent with the theory that they have arisen from a number of different lines of terrestrial insects, and not directly from the ancestral marine group. Here are some of the principal types.

Cutaneous respiration. This is the simplest respiratory mechanism, and is found in certain larvae of Diptera (*Chironomus*, *Simulium*) (Fig. 70), that of the genus *Acentropus* (Lepidoptera), and of several Coleoptera. All the spiracles are closed, and air diffuses through the integument. The larvae are therefore *apneustic* throughout their early stages, and the spiracles do not open until the mature larvae are ready to leave the water in order to pupate.

Blood-gills. These are rare in insects, and are seldom seen apart from the larvae of *Chironomus*, of *Catalysta fulicalis* (Lepidoptera), and of

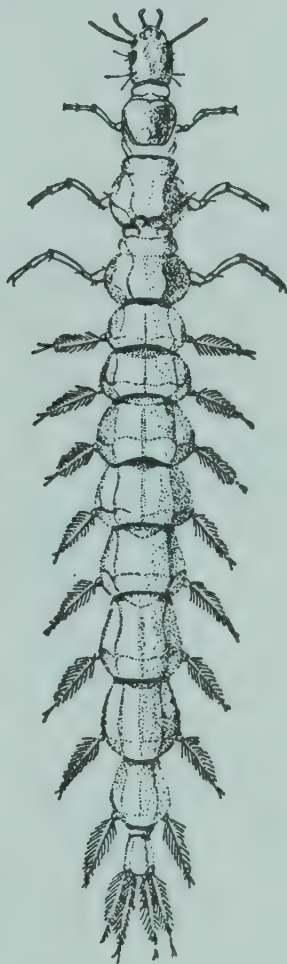


Fig. 71 – Larva of *Gyrinus marinus*, an aquatic beetle, with tracheal gills on all the abdominal segments (after SCHIÖDTE).

Hygobia tarda (Coleoptera). Blood-gills are simple evaginations from the body-wall, filled with blood, and apparently not specially adapted for respiration.

Tracheal gills. These are also evaginations from the body-wall, sometimes thread-like, sometimes plate-like, but always bearing a network of tracheae, through which the air moves by simple diffusion. This kind of gill in insects (Fig. 71) is not a place where exchange of oxygen takes place, as are the gills of fishes. It merely allows air to enter the tracheal system, just like an ordinary spiracle, and indeed may be present in addition to spiracles in many insects.

Tracheal respiration. Many aquatic insects come to the surface to obtain oxygen and their tracheal system has been modified to make this easier. Many of them are *metapneustic*, only the posterior spiracles (eighth pair) remaining open. The larva of *Dytiscus* (Fig. 72) obtains air by having its posterior spiracles surrounded by hydrofuge hairs, and supported at the water-surface by a pair of *urogomphi* developed for this purpose. The

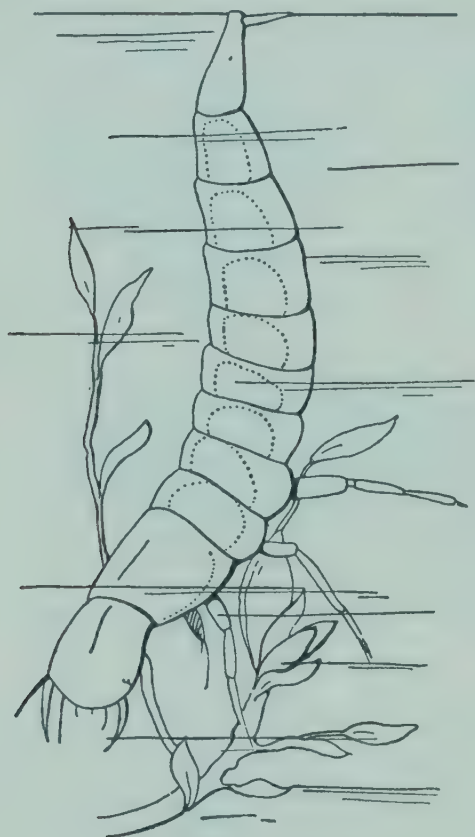


Fig. 72 – Larva of *Dytiscus* (Coeloptera) drawing air at water-surface (after KORSCHULT). Tracheal respiration.

larvae of *Eristalis* reach out to the surface with a long, extensible siphon from the posterior tip of the body, while the water bugs *Nepa* and *Ranatra* (Fig. 73) also have a respiratory tube. HYDROPHILIDAE use the antennae to draw air from the surface on to the ventral surface of the body, where it is retained by hydrofuge hairs, and forms a shining plastron of air.

All these mechanisms are made possible by the existence of oily or waxy secretions, which make the integument non-wettable. Anything which reduces the surface tension of the water defeats this mechanism, and this is the basis of the destruction of mosquito larvae by spreading a thin film of oil over the surface of the water.

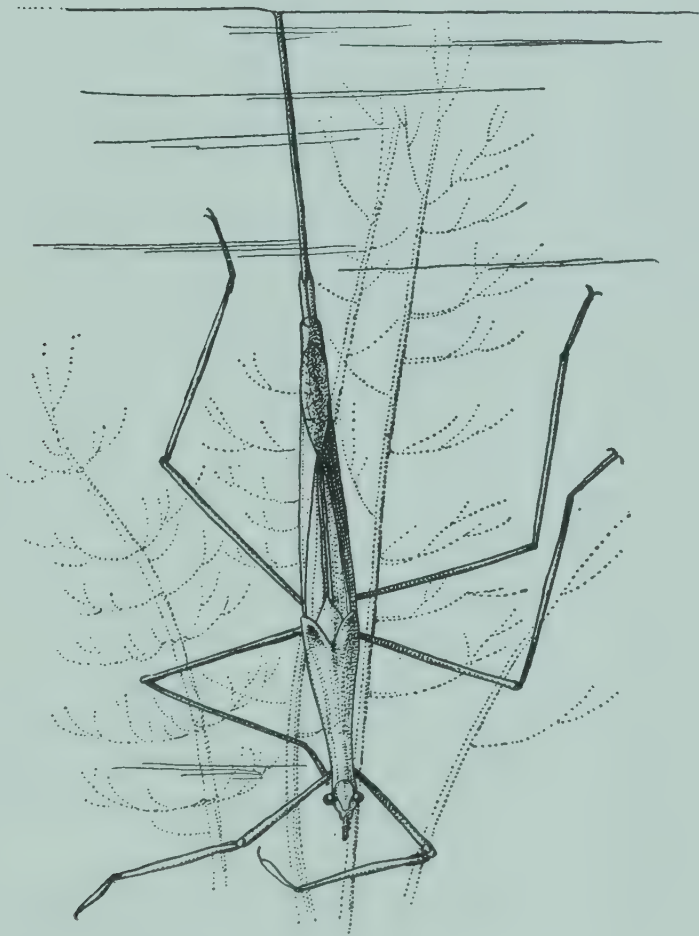
Those insects that swim actively beneath the surface, such as DYTISCIDAE, NOTONECTIDAE and CORIXIDAE, take down with them when they dive a reserve supply of air, trapped underneath the elytra, or held against the surface of the body by hydrofuge hairs. This air-bubble may sometimes act as a hydrostatic organ, allowing the insect to rise to the surface

without effort whenever it wishes, while at the same time the reservoir of air helps in respiration.

In the second capacity, the air-bubble is not merely a store of oxygen, but functions as a lung to extract more oxygen from the water. As the insect breathes, the oxygen in the bubble is reduced, and replaced with carbon dioxide. As the partial pressure of the oxygen in the bubble falls below that in the surrounding water, more oxygen diffuses into the bubble until equilibrium is restored. Meanwhile, however, the nitrogen, which takes no part in respiration, is slowly dissolving in the water, and reducing the volume of the air-reservoir. It is to replace this lost nitrogen, rather than in search of oxygen, that the insect has to come to the surface periodically.

Capture of oxygen from plants. Phytophagous insects may extract

Fig. 73 – *Ranatra linearis* (Hemiptera; Cryptocerata) replenishing its tracheae from the water-surface by means of its siphon.



oxygen from the tissues of submerged plants. Some examples of this habit are *Hydraena*, the DRYOPIDAE, *Lissorhoptrus* (CURCULIONIDAE), and *Donacia*.

The larvae of *Donacia* (Coleoptera: CHRYSOMELIDAE) are free-living on the submerged stems of aquatic plants. The spiracles of the eighth

segment carry a sort of spur (Fig. 74), which they stick into the aeriferous tissues of the plant. The larva is thus provided with a ready-made breathing apparatus, and need never come to the surface.

CIRCULATORY SYSTEM

The blood circulates through the general body cavity, or haemocoel. The contractions of the dorsal vessel cause the blood to move towards the head inside this tube, and movements within the haemocoel itself are produced by the undulation of diaphragms, and by the compression of the abdomen during its respiratory movements. Special organs (*pulsatory*



Fig. 74 – Larva of *Donacia* (Coleoptera; Chrysomelidae) (after BÖVING). This larva lives submerged in the water, and obtains oxygen by piercing the air-spaces of aquatic plants, by means of the spur on the spiracle of the eighth segment.

ampoules) assist the circulation of blood in the various organs, and especially in the wings, where each vein has a blood-space.

The blood. This can be referred to as a haemolymph, since it consists of a serum in which are suspended nucleated cells, or haemocytes, though it has no constituent that can act as a vector of oxygen. Generally it is colourless, but sometimes has a pigment. CHRYSOMELIDAE have the blood differently coloured in the two sexes, while the larvae of *Phytodecta quinquepunctata* have green blood in the females, and colourless blood in the males; those of *Galerucella luteola* have white blood in the females, but yellow in the males.

Many insects have toxic substances in their blood. The Meloidae have from 0.25 to 0.50 per cent cantharidin, which is a violent poison against humans, though much less so against insects. Those beetles that have toxic blood also sometimes show the phenomenon known as reflex bleeding (*autohaemorrhoea*, see Fig. 75), by which they can extrude drops of blood from the joints of the body.

Other beetles may accumulate in their blood the toxic substances that they take up from the plants upon which they feed; e.g. the Meloid

Epicauta ruficeps which lives on the plant genus *Strychnos* in Sumatra. In Africa a number of different CHRYSOMELIDAE are used by the natives as a source of arrow-poisons.

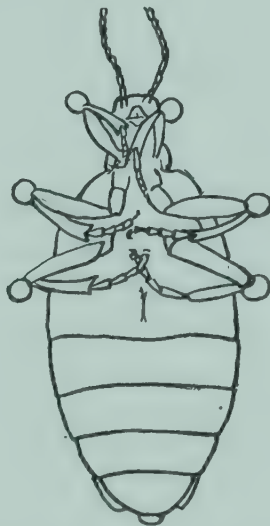
SENSE ORGANS

The physiology of the sense organs of insects has been intensively studied in recent years by many biologists, using methods that are often most ingenious. A variety of insects have been the subjects of these investigations, but the most remarkable results have been obtained by von Frisch, working on Honey-bees. From all these experiments the conclusion can be drawn that insects are far less aware of the outside world than are the higher vertebrates, and particularly than man.

Sight. Insects do their seeing—that is, their appreciation of images or patterns—by means of their compound eyes. The function of the ocelli of the frons is not known very precisely, but it appears that they may be organs of stimulation, controlling such activities of the insect as are influenced by light and darkness. Although the compound eyes are the true organs of vision, there is no doubt that many insects also possess a general sensitivity to light, distributed all over the body, since the eyeless insects, notably cave-dwellers, react readily to light which falls upon them.

Measurements have been made of the sensitivity of the compound eyes to light, that is to say, of the intensity of light needed to bring about a reaction of the insect, with specially designed apparatus. It has been estimated that the sensitivity to light of a bee is only one-tenth that of Man, and that of *Drosophila* only one-hundredth.

Fig. 75 - Reflex bleeding in *Meloe violaceus* (Coleoptera) (after LANGERKEN).



The compound eye of an insect, with its hundreds—or even thousands—of facets, conveys a multitude of different impressions to the brain, which combine to give a visual mosaic. An extensive field of view is covered, and those insects with large eyes, such as the dragonflies, can

see in nearly all directions, fore and aft, up and down, at the same moment. The construction of a single ommatidium shows that the image produced by one facet must be of poor quality, and it is generally agreed that by itself it can give only a blurred impression of shapes. There is no focusing mechanism, but the retinal cells are so deep that the image is always sharp somewhere along the length of the ommatidium. Evidently the insect can appreciate the position at which this occurs, and so can estimate how far away is the object at which it is looking. The insect has thus a precise measure of distance, not only by the stereoscopic effect of numerous images, but by an internal scale within each ommatidium. In addition a mosaic pattern of this kind is very efficient in detecting movement.

In short, an insect has a poor appreciation of shape, but an acute appreciation of movement, which (with few exceptions, such as Mantids) it can detect over a wide field of view without having to move its head.

It is known also that insects can perceive colours, but here again their vision differs considerably from our own. Kuhn and von Frisch, by patient training of bees to come to drink from dishes placed on different coloured surfaces, showed that bees are insensitive to red, which they confuse with green, like people who have Daltonian colour-blindness; but at the other end of the spectrum they are strongly sensitive to ultra-violet, which they see as an additional colour, complementary to blue-green.

Their imperfect colour vision is no doubt the explanation of some of the mistakes that they occasionally make. Often in summer, during the heat of the day, the Humming-Bird Hawk Moth, *Macroglossa stellatarum*, comes indoors, and tries to sip from flowers on the wall-paper, and I myself have observed a striking visual aberration in some Mason-Bees, which is all the more remarkable because it is accompanied by a keen sense of orientation by the sun.

At the Château de la Rolière, in the Drôme, a colony of these bees builds its nests all along a row of eight pointed arches, which are *painted* on a perfectly flat wall, and which consequently give no shelter at all to the nests. But the most surprising thing is that they only build their nests on those parts of the arches that would be in shade if the arches were real! The artist who painted this mural showed the weakness of his technique by painting the same amount of shadow on both sides of each arch, but the bees know better than this: they only build on the side that ought to be in shade. Thus we see that the defective vision of the bees modifies their behaviour only to the point at which it begins to conflict with their general sense of orientation to light, and that the latter is the dominating instinct.

Smell. Here again the sensitivity of the insect is of a different order from that of humans. Odours are detected by sensillae, simple or complex,

situated more especially on the antennae, but also on the palpi and sometimes in other parts of the body.

It has been found that some odours are attractive to bees, and some repellent, and that the insects are guided to flowers by scent as much as by sight. Ants from the same nest recognize each other by smell, which is passed on to them by the queen of each nest. This odour, which we cannot distinguish, persists for several months. Stranger ants which venture into a nest for which they have not the appropriate odour are

Fig. 76 - *Pachypus candidae*
(Coleoptera Scarabaeidae)
(after PAULIAN). Winged
male and wingless female.



furiously attacked, but this does not occur if the antennae of the resident ants have been removed; thus showing that the means of recognition by smell is located in the antennae.

The olfactory sense of insects is surprisingly acute, and is effective over great distances. Here we may recall the experience of Revélière, when he was collecting in Corsica. He noticed a number of males of the Scarabeid beetle *Pachypus cornutus* (Fig. 76) hanging upside-down from a bush close to the ground, and so he looked on the ground for the wingless female of this beetle, which is subterranean, and comes to the surface only in order to mate. When he found and picked up a female she squirted on to his sleeve a jet of the liquid which is secreted to attract the males. For several days afterwards males came and settled on his sleeve, even in the centre of the town, and far away from the regular haunts of *Pachypus*.

According to Warnke it is the antennae which detect odours from a distance (Fig. 77); the maxillary palpi have a range of round about a decimetre, and the labial palpi only a centimetre. He was able to establish that distant odours have a differential effect on the antennae, so that the insect is guided towards the source; when it comes nearer to the source of the odour the insect moves directly to it.

Smell plays a big part in bringing the sexes together for mating. In

many species, such as the *Pachypus* we have just mentioned, the females have glandular secretions which attract the males. The females of *Stylops* spend their lives immersed in the body of the bee or wasp that they parasitize, with only the cephalothorax (fused head and thorax) protruding. Here they bear glands, called the *glands of Nasonov*, which produce an odorous secretion to attract the males. The latter have emerged from another hymenopteran, perhaps a long way off, and without the help of an odour the meeting of the sexes would be almost impossible.

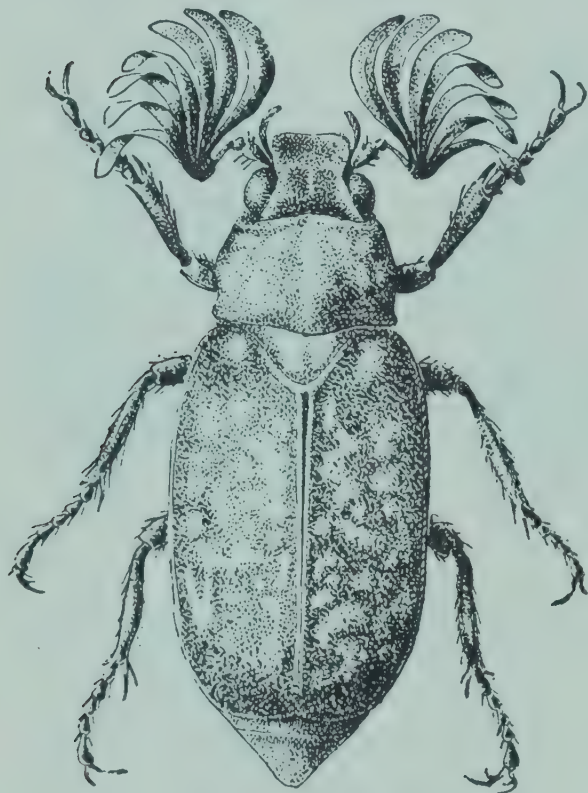


Fig. 77 – *Polyphylla fullo* (Coleoptera; Scarabeidae) (after PAULIAN). Male with large, flabellate antennae, in which the sense of smell is located.

Taste. Insects that browse, and chew their food, have the organs of taste distributed over the mouthparts—on the mandibles, the maxillae and the labium—and also in the pharynx, the epipharynx and the hypopharynx. Sucking insects, such as Lepidoptera and Diptera have organs of taste on the tarsi. Minnich conducted an experiment (Fig. 78) to show that if the fore-tarsus of a butterfly is touched with a solution of sugar the proboscis is unrolled; on the other hand a trace of quinine in the solution inhibits the reaction. Further experiments have shown that butterflies (*Pieris brassicae* or *Pyrameis cardui*) are very sensitive to sweet and bitter tastes, but not to salt.

The fly *Calliphora* is thirty times as sensitive to sugar as a human tongue. The taste of the bee for sugar differs from our own. It does not appreciate saccharine-like compounds, whereas others that seem more bitter to us are obviously sweeter to the bee. This is the case with acetyl-

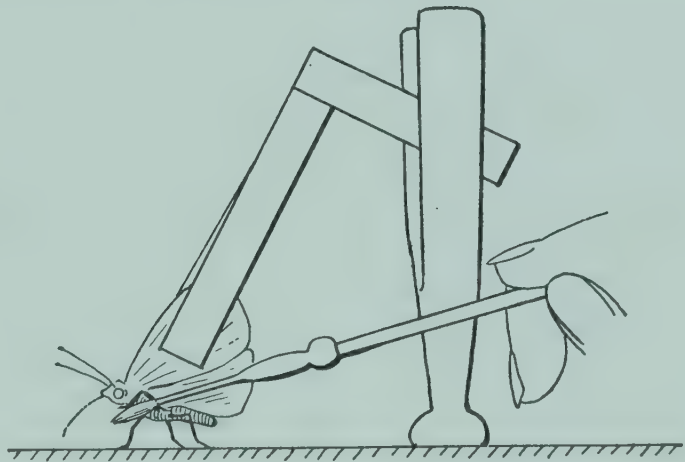
saccharose, which bee-keepers use to denature the honey that they give to their bees for winter food, and so to make it unpalatable to humans.

Thus, insects have an appreciation of degrees of sweetness that varies in different species, and which is greatest in omnivorous insects. It has been shown that among ants, *Myrmica rubra*, which is omnivorous, can distinguish many more different kinds of sugar than can *M. rubida*, which is carnivorous.

Hearing. If vision, smell and taste are the most highly developed senses in insects, hearing, on the contrary, seems to be rudimentary.

Receptor organs turned to one particular frequency of vibration have been demonstrated. The plumose antennae of male mosquitoes vibrate in response to certain notes, which are exactly those produced by the wings of the females and it has been stated also that ants react to sounds, provided that their antennae are intact. There must be, therefore, a range of sounds which can be detected by the antennae, but insects have, in addition, other sound-receptors, chordotonal organs, distributed over the body. Orthoptera have tympana on the tibiae or on the sides of the body, and these register vibrations in the air, over a range of frequencies quite different from that audible to the human ear.

Fig. 78 – MINNICH's experiment, showing that the sense of taste is located in the tarsi in butterflies (after MINNICH). If the fore tarsus is touched with a brush dipped in a sugar solution the butterfly unrolls its proboscis.



Observations have been made on a variety of species. According to Chauvin, caterpillars of Lepidoptera react to frequencies between 32 and 1,024 vibrations per second. Cockroaches respond to bass frequencies too low for the human ear, and in the opposite direction go up to 3,000 per second. The thoracic tympanum of grasshoppers seems to respond to sounds beyond our audible range, and certain Katydidids have been measured up to 45,000 cycles per second.

Despite the wide range of frequencies covered, the sounds to which insects listen seem to be simple ones. These are the sounds produced by stridulating organs, which are widely distributed through the insect world, and which generally rub some part of the body against a ridged surface

(Fig. 79). In contrast to these are the drum-like organs of Cicadas and some Lepidoptera, in which a stretched membrane is set in vibration by the play of muscles.

Stridulatory organs generally occur in males, and are used to attract the females, but not a few insects have them in both sexes, which can

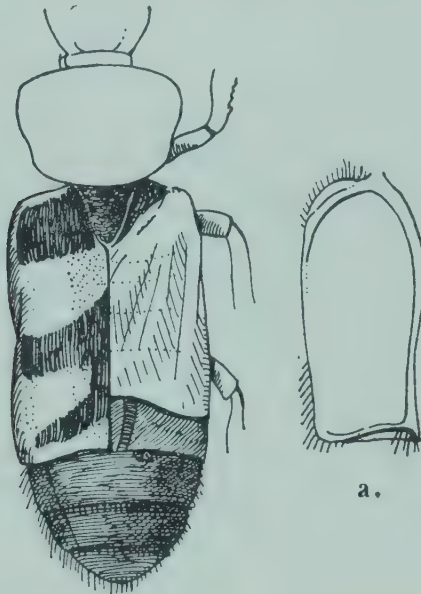


Fig. 79 – Stridulatory apparatus of *Necrophorus* (Coleoptera) (after WEBER).

then respond to each other. According to Ohaus, American *Passalus*, beetles related to the LUCANIDAE, live in families under the bark of dead trees, and communicate with each other audibly. Within each colony the adults summon the larvae together by stridulating, and the larvae reply by making a noise with their feet. To be precise, the larvae of *Passalus* have a ridged surface on the mid-coxae, upon which the claw of the very short hind-leg scrapes, like someone playing on a mandoline (Fig. 80).

Other senses. The sense of touch is exercised chiefly by the antennae, held forwards and tapping the objects that are being inspected. Many carnivorous beetles (*Anthia*) seem to be able to find their prey only by blindly feeling for it. In addition, contact with certain local areas of the body may produce a reflex response (reflex immobility, thigmotactic reflex), to which we shall return later.

It has often been suggested that insects can appreciate their surroundings by the use of special senses for which there is no human equivalent. There is no evidence for this belief. The truth is that neither in hearing, sight or smell do the insects respond to quite the same range of sensations as human beings, and in these senses they are aware of stimuli that are outside our perception; but nothing leads us to believe that they enjoy sensations that are different in character from our own experience.

The 'topochemical' sense in ants, of which we have spoken above, is

no more than a highly refined sense of smell, which has directional properties. The human eye and ear have this directional property, and can orientate themselves towards the source of sensation, but our noses can only do so very imperfectly. It would seem that the location of the olfactory organs on the antennae of insects enables them to track down a smell with the same precision as sight or hearing.

TROPISMS

Phototropism. It is well known that many insects move towards the light. For a long time it was thought that their movement was more or less purposive, but the American biologist, J. Loeb, showed that it was a phenomenon allied to the heliotropism of plants. The action of light on the living tissues produces automatic reactions, which first turn the animal in relation to the source of light, and then cause it to move either towards the light (positive phototropism) or away from it (negative phototropism).

The degree of phototropism varies in different species, and can be estimated by the extent to which the movement of the animal departs from a straight line. An animal that is strongly phototropic moves as if it were 'threaded on to the ray of light'; one that is only weakly phototropic moves in a zig-zag path, by a series of approximations, as if the orientation derived from the light was easily lost by each chance deviation. All degrees of phototropism occur, and many animals show no reaction to light at all.

How does the light act on the animal? Clearly by a photochemical stimulus, controlling the reflexes of movement, and primarily serving to point the animal in the right direction. This occurs not only in animals

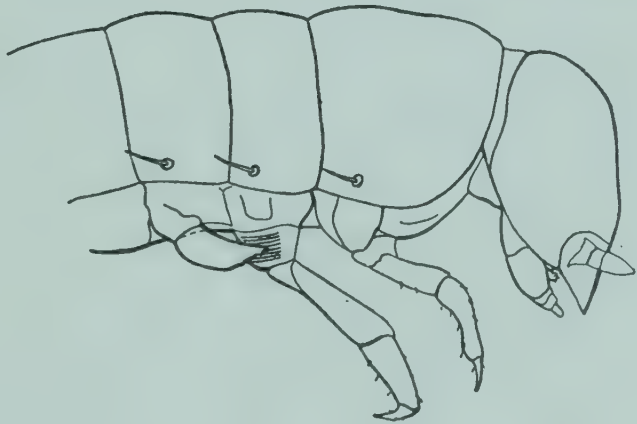


Fig. 80 – Stridulatory apparatus of the larva of *Passalus* (Coleoptera) (after PAULIAN). The hind-leg is small and mis-shapen, and rubs against a set of ridges on the coxae of the middle leg.

with eyes, but equally in eyeless ones. The ability to detect light is a property of all living matter, so that there is a photosensitivity diffused over the integument, as well as that which is specially concentrated in the eyes.

As well as differing among different species, phototropism also varies in the same individual under varying conditions. Generally speaking, a

rise of temperature increases the sensitivity to light. In certain animals of negative phototropism, a fall of temperature makes their reaction positive, and the change is abrupt. Phototropism is also subject to internal influences. Caterpillars of *Porthesia chrysorrhoea* are positive at the moment when they are immature, and first come out of winter diapause, so that they climb up the trees and feed on the spring shoots. As soon as they are fully fed they lose their phototropism, and so are able to come down again and disperse.

The state of maturation of the gonads evidently plays a part in determining phototropism. As a general rule a positive phototropism occurs in sexually mature individuals, and this phenomenon seems to contribute to the nuptial flight of ants, bees and termites, as well as in other aspects of the biology of these social insects.

Phototropism is concerned with the sum total of movements that are orientated in relation to the direction of the light; other reactions depend simply upon the intensity of illumination. If the animal makes a choice between light and shade it is said to show *differential sensitivity* (J. Loeb).

Light and shade have their effect upon all the vital activities, the daily rhythm of waking and sleeping, and all the complex rhythms of the various organs. Some insects seek the light, and their ocelli act as organs of stimulation in the presence of light; others, on the contrary, shun the light and retreat to shady or dark places. This choice between light and dark is called *phototaxis*, and according to Loeb there is a fundamental difference between phototropism, which is a phenomenon of orientation, and phototaxis, a phenomenon of choice. Phototaxis may, of course, be positive or negative.

The classification proposed by Kuhn has complicated matters. *Phobotaxis* is no more than a differential sensitivity to light intensity. Kuhn distinguishes *scototaxis*, which is seeking the light, and *photophobotaxis*, seeking darkness, corresponding to our positive and negative phototaxis. The only thing that is new in Kuhn's work is to define *menotaxis*, when the animal moves at a constant angle to the direction of the light (light-compass reaction). This is what makes insects circle round a lamp, as has long been known.

Thermotropism. There is no thermotropism, in the strict sense, among insects. It has been recorded that the bug *Rhodnius prolixus* is attracted by sources of heat, but it has been shown also that it does not orientate itself in relation to thermal radiation. Guided by its antennae, the bug selects a place where the air is warmest, and is therefore showing the phenomenon of thermotaxis.

Insects are *poecilothermic*: having no mechanism for regulating the body temperature, they are at the mercy of external fluctuations. The warmer it is, the more active they become. The relation between tempera-

ture and activity follows the law of Arrhenius, which states that metabolic reactions go on at a rate which doubles for every ten degrees' rise in temperature, up to a critical point of 43° C., when it stops, this being the maximum that can be tolerated. Although they cannot control their temperature directly, insects avoid being frozen in winter, and can protect themselves against excessive summer heat, by making use of their thermotaxis, to choose situations favourable to themselves.

The deserts are the hottest environments. Buxton, experimenting on desert insects in Palestine, states that the temperature of the soil surface may reach 60°–65° C. Carabid and Tenebrionid beetles are extremely active under these conditions, running with an extraordinary speed, raised up on their legs, holding the body as far away as possible from the hot ground. Whenever the air temperature is too high for them, the insects burrow into the sand, or into the holes of reptiles and small mammals. Thirty centimetres below the surface the temperature is uniform, never rising above 30° C.

When the ground temperature is 45° C., the internal body-temperature of a *Blaps* or a *Pimelia* does not exceed 39°–40° C. so long as the insect is alive, though it goes up to 45° C. when the insect is dead. This small difference is caused by evaporation of water during respiration. Buxton also stated that black insects were often 4°–5° C. higher in body-temperature than pale ones.

Some insects live in hot-springs (Diptera, DYTISCIDAE, HYDRAENIDAE), but as a general rule one can say that none of them can tolerate a temperature in excess of 43° C.

Hygrotropism. The humidity of the atmosphere has a great influence on the activity of insects, especially nocturnal ones. It is the humidity, rather than the temperature, that governs the activity of Lepidoptera. There are nocturnal Lepidoptera that fly only when it is raining, and *Cochylis* and *Eudemis*, parasites of the vine, do not appear in light traps unless the humidity is high. The swarming of nocturnal insects round the lights on thundery evenings is largely brought about by the high humidity, though no doubt static electricity also plays a part.

Although the importance of humidity to the insects can be inferred we are without precise information about it, and no one knows which organ is sensitive to variations in humidity in the air. It has been suggested that the antennae may be involved.

Chemotropism. We have shown above that smell has a great effect on the behaviour of insects. The antennae are sensitive to odours to a degree far beyond that of the human nose, and in addition they give a directional effect, so much so that we speak of special sense, the topo-chemical sense. The insect detects odours at a considerable distance, and finds its way to the source by tapping, and a process of trial and error.

PLATE 2 – I. THE COPULATION OF INSECTS

A. **Saga ephippigera** (Orthoptera; Tettigoniidae)
(after BOLDYREV).

B. **Pezotettix giornai** (Orthoptera; Acrididae)
(after CHOPARD).

C. **Bupalus piniarius** (Lepidoptera: Geometridae)

D. **Pulex irritans** (Aphaniptera) (after MEISENHEIMER).

E. **Bittacus tipularius** (Mecoptera: Bittacidae)
(after BRAUER).

PLATE 2-I. THE COPULATION OF INSECTS



PLATE 2 – II. THE OVIPOSITION OF INSECTS

- A. Female of the Woolly Aphis (**Schizoneura lanigera**), bearing only a single egg.
- B. The same in the process of egg-laying.
- C. A female termite with its abdomen enormously distended by thousands of eggs.
- D. The fly **Dermatobia cyaniventris** has laid a clutch of eggs on the abdomen of **Stomoxys**. When this *Stomoxys* bites a mammal, the larvae of the *Dermatobia* will have already hatched, and will drop on to the skin of the mammal, afterwards forming erupting tumours on the skin.
- E. Male of **Phyllomorpha laciniata** (Hemiptera), bearing the eggs laid upon it by others of the same genus.
- F. A leaf cut by the female of **Deporaus betulae** (Curculionidae), which waits for it to wilt before rolling it into a cigar-shaped case.
- G. The finished case, in which **Deporaus** has laid its eggs.
- H. An egg-mass of **Tabanus quatuornotatus** (Diptera).
- I. An egg-mass of **Panolis flammea** (a Noctuid moth).
- K. An egg-mass of a Pentatomid bug.
- L. An egg-mass of **Malacosoma neustria** (Lepidoptera: Lasiocampidae).
- M. **Schistocerca gregaria**, a North African migratory locust, laying its eggs in the ground.

PLATE 2-II. THE OVIPOSITION OF INSECTS

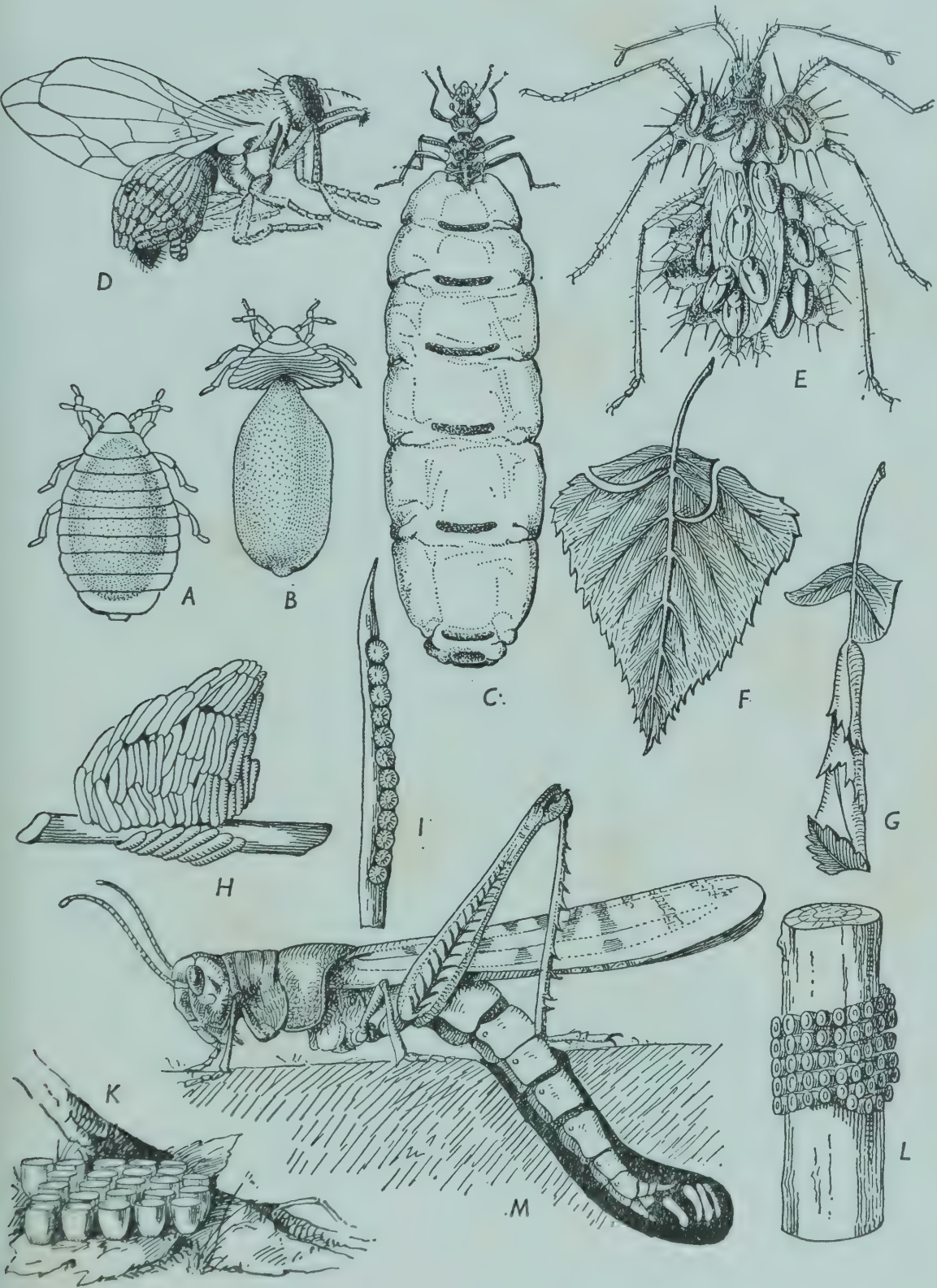


PLATE 2 - III. CRYPTIC COLORATION - LEAVES

1. A group of leaf-insects, **Phyllium bioculatum**, among foliage. The male, female and second stage larva are green; the newly-emerged larva is red.

2. **Onomarchus leuconotus** (Tettigoniidae), from Tropical America.



IV



PLATE 2-IV. CRYPTIC COLORATION-
TWIGS AND BARK

1. **Dixippus validior**, a Phasmid imitating twigs.
2. **Trachyzulpha frühstorferi**, a Pseudophyllid,
imitating lichens.
3. **Sathrophyllia femorata**, A Javanese long-horned
grasshopper, imitating bark.

When it gets near enough it gives up searching, and goes straight towards its goal.

Thigmotropism. We also give the name *stereotropism* to the tendency shown by many insects to press a given part of the body against a solid surface. This is the mechanism by which so many insects protect themselves by hiding under stones, tree-trunk and bark. The vivarium of the Jardin des Plantes provides a practical demonstration of this fact: scorpions can be seen lying immobile under a sheet of glass, thus showing that when they normally hide under stones they are not retreating from the light, but are satisfied with the sensation of having a hard surface pressed against the dorsum of the body.

Thigmotropism plays an important part in the life of many insects. As a positive reaction it brings about the gregarious assembly of Hymenoptera or of Coccinellids, often seen at the approach of winter; as a negative

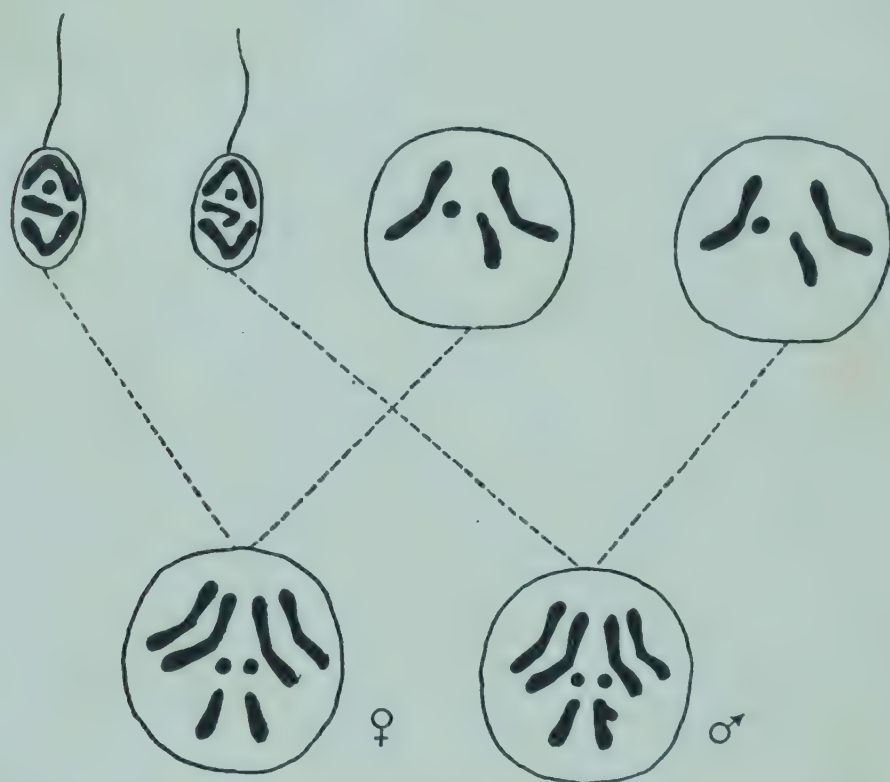


Fig. 81 - Diagram showing sex-determination in *Drosophila*, which is the same as the human type. There are two sorts of spermatozoa, those with an X (the intact heterochromosome), and those with a Y (the bent, inactive heterochromosome). The sex of the egg is determined at the moment of fertilization.

one it causes leaf-feeding insects to fall to the ground when they are disturbed, and serves to overcome the reflex immobility that we shall be discussing later on. Under this heading, too, comes the reflex shedding of limbs by Orthoptera.

REPRODUCTION

Sex-determination. Sex is determined in the egg, and is decided by the arrangement of chromosomes. In every cell of an individual animal there are a number of pairs of chromosomes that are the same in both sexes (*autosomes*), and one pair that differ in the two sexes (*heterochromosomes*,

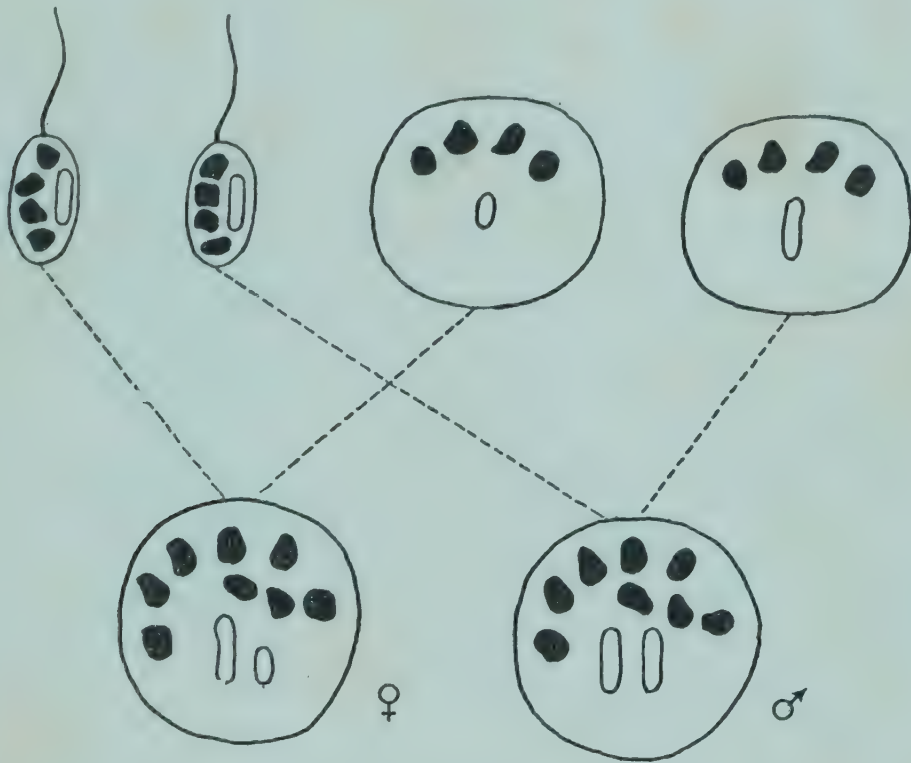


Fig. 82 – Diagram of sex-determination in the butterfly *Abraxes* (bird type). There exist two sorts of ova, those with a Z (long, intact heterochromosome) and those with a W (short, inactive heterochromosome). The sex of the egg is therefore predetermined in the ovum.

or *sexual chromosomes*). In one sex the two heterochromosomes are alike; in the other sex one of the heterochromosomes is reduced, and inactive, or may be totally absent. In this respect insects fall into two groups.

The first group have the *human type* of sex-determination: these include Coleoptera, Orthoptera and Diptera, notably *Drosophila*. At the reduction division, all the ova produced by the females receive their stock of autosomes (A) and one heterochromosome (X), thus: ($A+X$). But in the male, half of the spermatozoa receive an active heterochromosome ($A+X$), while the rest receive only an inactive heterochromosome (Y), becoming ($A+Y$). Thus, there is only one kind of egg, but two kinds of sperm, which combine to give females ($2A+2X$) and males ($2A+XY$) in equal numbers (Fig. 81).

In the other group the *bird type* of sex-determination obtains, which obtains also in birds, worms, mollusca, crustacea, fish and so on. Here

the heterochromosomes are paired in the male sex. This occurs in Lepidoptera and Hemiptera. Here there is only one kind of sperm, all having an active heterochromosome (Z), while there are two kinds of egg, those with an active heterochromosome (Z), and those without Z , or with an inactive heterochromosome (W). The pairing ($2A+2Z$) now produces a male, whereas the pairing ($2A+WZ$) or ($2A+Z$) produces a female (Fig. 82).

We see, therefore, that whereas in the human type the sex of an individual is determined at the moment of fertilization, in the bird type the sex is predetermined in the ovum from the time of the reduction division.

Extensive observations on *Drosophila* have shown that what really determines the sex is the proportion between the amount of chromatin in the autosomes (A) and that in the heterochromosomes (X). When the proportion $X/A=1$, the sex is female. If, as a result of an accident, the proportion should be more than 1:1, then the insect is still female, but with the sexual characteristics exaggerated (*superfemale*).

When the proportion $X/A=1/2$, the sex is male. Again, as a result of an accident during cell-division the proportion may fall lower, say to $1/3$ and in that event we get *supermales*. On the other hand, when the proportion X/A is intermediate between $1/2$ and $1/1$ the sex is intermediate; the individual is an *intersex*, with a mixture of characters of the two sexes. This is the case when, as a result of faulty division, we have triploid individuals, with three sets of autosomes but only two pairs of heterochromosomes ($X/A=2/3$).



Fig. 83 – A bipartite gynandromorph of *Pseudometoca canadensis* (Hymenoptera; Mutillidae) (after EIDMANN).

Sometimes there occurs an individual of quite a different type, male in some parts of the body and female elsewhere, known as a *gynandromorph* (Fig. 83). These are always produced from a female ovum, with two X-chromosomes. After embryonic development has gone some way certain cells accidentally lose one of their X-chromosomes, and consequently all the structures that arise from division of these cells are male in character. If the accident happens at the first division of the egg, the

insect is half male, half female (a *bipartite* gynandromorph); if the accident happens later on, the male characteristics appear in more limited areas (a *mosaic* gynandromorph).

It is important not to confuse intersexes and gynandromorphs with

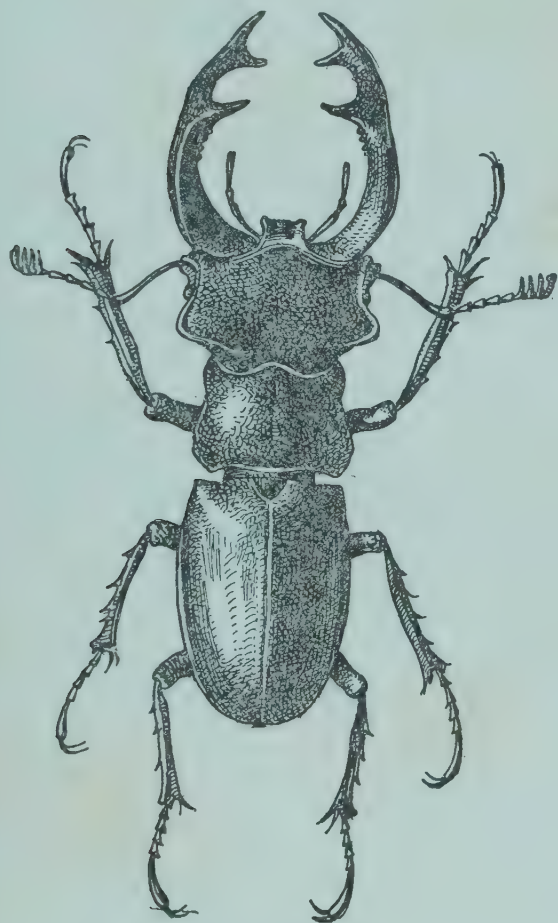


Fig. 84 – *Lucanus cervus*, male and female, showing sexual dimorphism.



true *hermaphrodites*, which have the characteristics of both sexes all over the body at different times. An example of genuine hermaphroditism is known in *Termitostroma schmitzi*, a strange termitophilous fly which passes in turn through a male phase and then a female one.

Parthenogenesis. The development of unfertilized eggs is quite common among insects, and then the generations may succeed one another for a longer or shorter time, without the appearance of any males at all. There is a kind of accidental parthenogenesis in which an unfertilized egg begins to develop, perhaps continuing to the larval stage, but rarely extending to the adult. If the insect has the bird type of sex-determination, the eggs are of two kinds, and therefore give rise to both males and females (*amphitokous parthenogenesis*).

It is more common, however, for the unfertilized eggs to give rise only to females (*thelytokous parthenogenesis*). Species may keep themselves going in this way indefinitely. When rearing *Carausius morosus* you may

not see more than one male among 3,000 females, and there are species of which the males are unknown in nature (e.g. *Phylloxera vastatrix* in Northern France, and *Adoxus obscurus*). Among Aphids, and other insects with a complex life-cycle, sexual generations may alternate with a series of parthenogenetic ones. In thelytokous parthenogenesis there is no reduction division during the maturation of the ovum, and the expulsion of the second polar body does not take place.

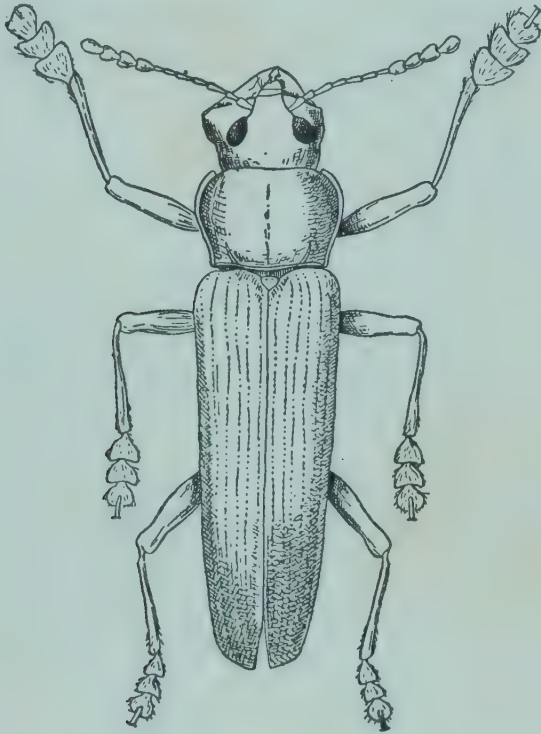


Fig. 85 – *Doubledaya viator* (Coleoptera: Languriidae) (after VILLIERS). Sexual dimorphism produces a strange asymmetry of the head in the female of this beetle.

Finally, a third type of parthenogenesis is called *arrhenotokous*, i.e. 'male-producing'. It is particularly associated with bees, where the unfertilized eggs give rise to drones. Since the bee has the human type of sex-determination, it is hard to see how an unfertilized egg (therefore haploid: $A + X$) can give rise to a male (diploid: $2A + X$). No one has yet demonstrated by what mechanism part of the X-chromatin is eliminated.

Sexual characteristics. There are many insects in which no external difference can be seen between males and females, except those which can be demonstrated by biometrical methods. In many cases, however, there are sexual characteristics, sometimes in the males, sometimes in the females (Fig. 84). Almost all the external features may be concerned in male sexual characteristics, which may be divided into those which have an obvious utility in finding a female or in mating (development of the eyes; the leaf-like antennae of *Lamellicornia*; tarsal dilations; special development of the wings; and so on) and those which have no obvious value. The great majority of sexual characteristics fall into the latter

category of the apparently ornamental (colour, sculpture, swellings and prominences, exaggerated size of organs, etc.).

The same may be said of the females, that some of their sexual characteristics are clearly associated with mating or egg-laying, while others have no obvious purpose, such as the extraordinary asymmetry of the head in the beetle *Doubledaya* (LANGURIIDAE) (Fig. 85).

These sexual differences are further complicated by the fact that there may exist more than one type of male (*poecilandy*) or of female (*poecilothely*) in the same species. The butterfly, *Papilio dardanus*, which occurs throughout tropical Africa, has more than forty different kinds of female, each of which is localized and mimics a local species of DANAIDAE.

Mating (Pl. 2, I). The sexes are brought together by a variety of stimuli. Many Orthoptera make sounds by the use of stridulating organs, and these are detected by tympanal organs situated on the tibiae and on the sides of the body. If the song of grasshoppers is not generally being used for mating purposes, there is no doubt that the Cricket calls females, and attracts them to him, by stridulation.

Female glow-worms send out light-signals, to which males respond in the same way, and it has been claimed that the intensity of the light changes when a male and female sight each other, the rhythm of their flashing becoming synchronized.

The females of some insects have glands which produce an odour



Fig. 86 – Copulation in *Empis* (Diptera) (after WEBER). Left, the male carries a cocoon in which he had enclosed the prey that he is about to offer to the female; right, copulation, with the female holding the cocoon that has been offered to her.

and may attract males from a long way off. The males of SATURNIIDAE, CETONIINAE, and those of *Pachypus cornutus* (Lamellicornia) can detect the scent of the female at a considerable distance. The sense of taste serves a similar purpose in Orthoptera.

PLATE 2 – V. CRYPTIC COLORATION – BARK AND
STONES among species from France and Algeria

1. **Phalera bucephala** (Lepidoptera), concealed upon a piece
of wood covered with lichens.
2. **Hyloicus pinastri**, a Sphingid moth, on the bark
of a tree.
3. **Eremocharis insignis** (Orthoptera), a desert species,
which imitates stones.

V



1



2



3

VI



1



3



2



4



5



6



7

PLATE 2 – VI. MIMICRY

Examples of Batesian mimicry

Aegeria apiformis (1), a harmless moth, mimics the Hornet, **Vespa crabro** (2), a Hymenopteron that is protected by its sting.

Polymorphism among the mimetic females of **Papilio dardanus**. The male (3) is always of the same type throughout Africa.

In Kenya Colony, the female of the form *trophonius* (4) mimics the Danaïd *Danaus chrysippus* (5), which occurs in the same locality.

In West Africa, the female of the form *hippocoön* (6) mimics the Danaïd *Amaurus niavius* (7), living in the same places.

In this way there are about forty different forms of the female of the same species, mimicking the Danaïds in different parts of Africa.

Finally we may mention the nuptial dances, by which swarms of small Diptera or Ephemeroptera rise up into the evening sunshine. In this connexion undoubtedly the most curious occurrence is the mating of *Empis* (Diptera), when the male presents the female with prey, wrapped in a ball of silk, or even with a ball of silk alone, which he brings with him as a wedding-gift (Fig. 86).

Oviposition (Pl. 2, II). The number of eggs laid by insects is extremely variable. The female of the Woolly Aphis lays only a single egg as big as herself, and after laying it she is left like an empty bag. Pl. 2, II (A, B). The female termite in her royal cell, lays millions of eggs in her lifetime. Pl. 2, II (C). The Tsetse fly produces a total of eight to ten young, one at a time, whereas each of the many eggs that the Chalcid *Ageniaspis fuscicollis* lays upon those of *Hyponomeuta* produces several hundred larvae by polyembryony.



Fig. 87 – Female of *Ligidura riparia* (an earwig), tending her eggs (after CHOPARD).

Many insects just drop their eggs on to the ground and abandon them, or put them under stones, or on the leaves and stems of plants, fixing them there with a sticky secretion. Some even place their eggs on other individuals of the same species. The eggs of *Phyllomorpha* (Hemiptera) while matching perfectly in colour when they are laid on *Paronychia*, are brilliantly golden when they are laid on others of their own genus, and then glisten in the sun. Pl. 2, II (E). The males of the giant tropical water-bugs *Belostoma* carry the eggs on their backs. Lastly, the fly *Dermatobia* sticks its eggs on to the abdomen of biting flies, mosquitoes and *Stomoxys*, with the result that they are carried to mammals, which they parasitize. Pl. 2, II (D).

The great majority of insects, however, have some form of ovipositor,

or terebra, with the help of which they are able to place their eggs in a sheltered place. ACRIDIDAE dig a deep hole, into which they insert the whole abdomen, and there lay a batch of eggs surrounded by an ootheca, or pod. Pl. 2, II (M). Other insects make use of their ovipositor to pierce the tissues of plants, and so to place the eggs inside the material upon which the larvae will feed. It would take too long to list all the devices used by different insects to make sure that their larvae are protected: excreta gummed together with secretions to make a shelter; the ootheca of Mantids and Blattids; the egg-cocoon of Hydrophilids; nests of leaves rolled into cigars by *Apoderus* and *Attelabus* (CURCULIONIDAE), Pl. 2, II (F, G); burrows of the predaceous Hymenoptera, which they provision with paralysed prey before laying their eggs in them.

All the behaviour-mechanisms of insects at the time of egg-laying are directed towards the preservation of the species, but in spite of this there is no guarantee of safety for the eggs, exposed as they are to extremes of temperature, as well as to the attacks of predators. The number of eggs laid is related to the risks they run, and is the best assurance of the survival of the species. Pictet has calculated that in certain Lepidoptera more than 99 per cent of the eggs laid are either destroyed, or if they hatch into larvae, these fail to reach maturity. Yet these Lepidoptera thrive in nature, their enormous egg-production compensating for these losses.

Care of eggs and larvae (Pl. 2, VII). Even the insects that take precautions in laying their eggs in a safe place do not always abandon them there. Many species cover their eggs and then remain with them, to protect and feed the young larvae. Some insects show a maternal instinct nearly as highly developed as that of mammals or birds.

The female of the earwig *Labidura* lays its eggs under a stone, and remains with them, licking them constantly to forestall the development of dangerous moulds (Fig. 87). After they have hatched, the mother remains in her den surrounded by a milling crowd of young ones. Carabid beetles have similar habits. In summer, in the mountains of Bihar, you may find females of *Molops piceus* retreated into hollows under the big stones, with eight or ten larvae pressed against them, remaining thus until the second instar, without showing any tendency to cannibalism. Similar observations have been made in the Alps on *Oreophilus multipunctatus* by Boldori.

This is the highest level of maternal instinct in the Coleoptera. Coprophagous beetles (*Copris*, *Gymnopleurus*, *Geotrupes*) bury in deep holes a store of food that is partly intended for their larvae. Pl. 2, VII (C-F). The two sexes collaborate in this task, rolling the balls of dung, digging the hole, and shutting themselves up there with their provisions and their young.

Necrophagous insects bury carrion: the female cuts off fragments

PLATE 2-VII. CARE OF THE YOUNG

A. Female of the Hydrophilid **Hydrous piceus**, finishing off the cocoon that surrounds her eggs, and hiding it underneath a leaf floating on the water-surface (after MIGER).

B. Female of **Phytodecta rufipes**, a Chrysomelid beetle, with the young larvae that she has assembled on a branch (after LÜHMANN).

C. Galleries and oviposition chambers of the Scarabeid beetle **Onthophagus nuchicornis**, beneath a cow-pat. The burrow on the left has two upward branches: one allows the female to carry the sand from her digging operations up to where the male, remaining on the surface, occupies himself in spreading it out; the other leads into the cow-pat, where the female collects the material that she stores in the lower chambers to feed her larvae (two chambers are cut open to show a larva and an egg). In the middle a female is digging a burrow and carrying the sand right through the cow-pat, to discharge it above. In the burrow on the right the branch for taking away the waste sand runs along the surface of the ground, beneath the cow-pat (after BURMEISTER).

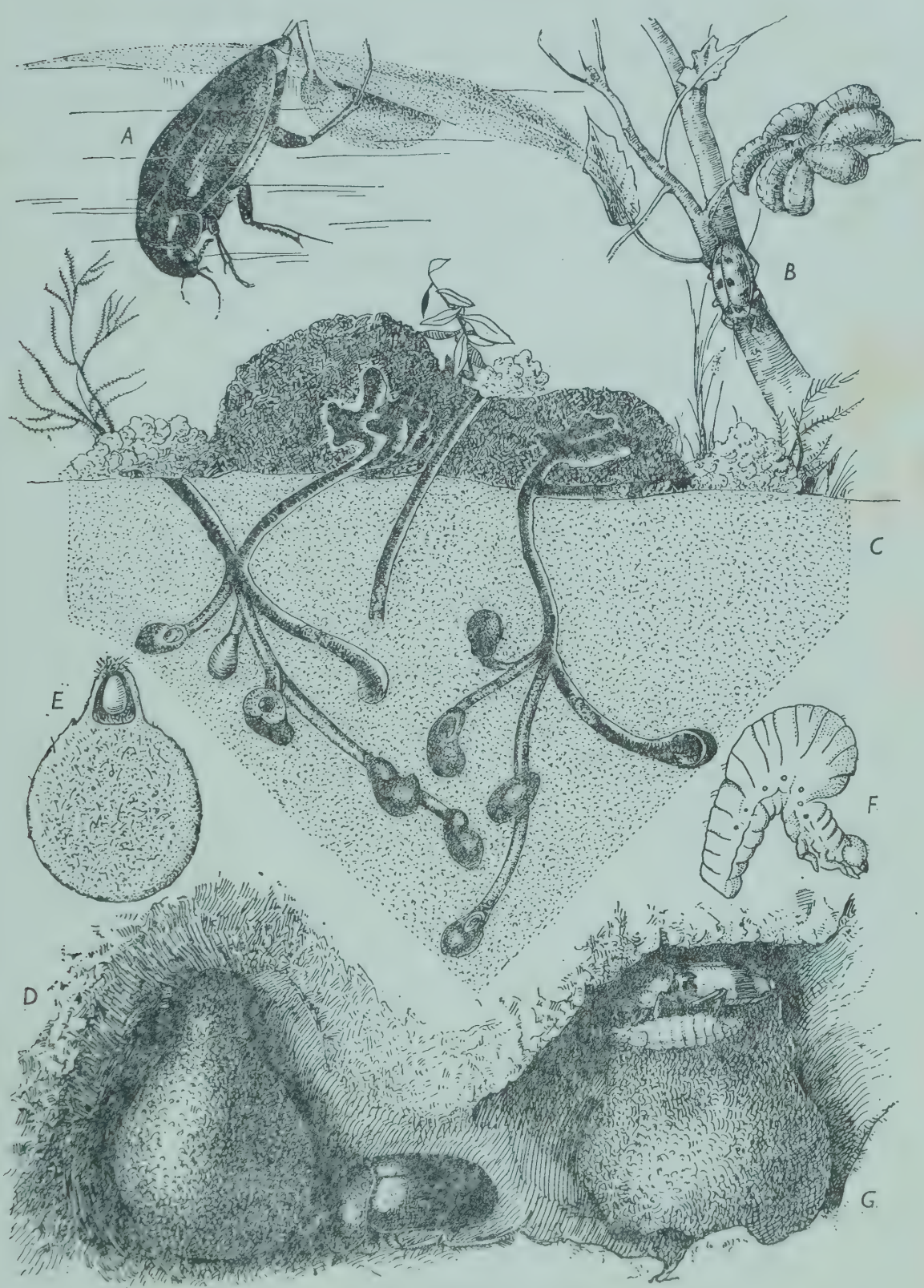
D. Female of **Scarabaeus semipunctatus** (Coleoptera) with the pear-shaped mass of sheep's dung, in which it has enclosed its egg and concealed it in an underground chamber.

E. A section of the 'pear', showing that the egg is in the narrow part, and is separated from the outside by a cap of vegetable fragments.

F. A larva of **Scarabaeus**, in side view, showing the curious swelling of the middle part of the body.

G. Female of **Necrophorus vespillo**, a Silphid beetle, feeding its larva, which lies on its back on the surface of the ball of carrion that is buried with it.

PLATE 2-VII. CARE OF THE YOUNG



and masticates them into pellets, which she stores in an underground tunnel, along which she lays her eggs. Until the eggs hatch the female remains on the food-pellets, and the newly-hatched larvae join her there, to be fed upon the regurgitated contents of the fore-gut of their mother. Pl. 2, VII (G). This stomodeal food is essential for the new-born larva, as well as at the later stages.

This behaviour of the females of necrophagous beetles may be compared to that of many social insects, which practise *trophobiosis*—that is, the exchange of food material between individuals, whether they are adults in the same nest, or parent and offspring.

7

Behaviour

SIMPLE BEHAVIOUR-PATTERNS

Walking. The legs are the organs of locomotion *par excellence* but some insects that have legs do not use them for walking. J. H. Fabre described how larvae of CETONIINAE crawl on the back. If these larvae find themselves accidentally outside their burrow, on the surface of the ground, they may be seen to turn over on their backs, legs in the air, and to move quickly along by undulations of the whole body. Other Scarabeid larvae (HYBOSORIDAE) move in the same way, but on their sides, without making use of their legs.

In contrast to this, many insect larvae crawl along, using their legs part of the time, and various abdominal locomotor organs in addition. The caterpillars of Lepidoptera, and those of sawflies, have abdominal prolegs. The larvae of Coleoptera often have the anus mounted on a tubercle, and equipped with eversible vesicles, often armed with crochets. This, then, constitutes a *pygopod*, which grips the substratum, and which the insect, when in motion, keeps bringing forward by contraction of the abdomen, and re-attaching in a fresh place. Lampyrid larvae (Glow-worms) have a pygopod of this nature which is sometimes used for locomotion, and sometimes for wiping and brushing the surface of the body of the insect.

Jumping. Many insects move forward in leaps and bounds, and most of them use the hind-legs for this purpose, with the femora specially long and thick. As a first step the tibiae are closed tightly against the femora, and then, by a sudden contraction of the femoro-tibial extensor muscles, the insect is projected violently upwards and forwards.

Very long jumping legs are well known in grasshoppers. Among beetles *Orchestes* (CURCULIONIDAE), *Altisa* (CHRYSOMELIDAE) and *Scirtes* (HELODIDAE) also have swollen femora which are used for jumping. Yet swelling of the femora is not always associated with jumping. *Sagra* (CHRYSOMELIDAE, Fig. 88) and the males of *Oedemera* have enormous femora, but do not jump; on the other hand the frog-hoppers (CERCOPIDAE) jump most vigorously, yet their femora are no more swollen than those of bugs that do not jump.

ELATERIDAE (Coleoptera), commonly called 'click-beetles', jump by a trigger-action of the prothorax. These beetles live on plants, and if they

fall to the ground their short legs make it difficult for them to right themselves once they are lying on their back. The insect turns itself over by 'looping the loop': a long extension of the venter of the prothorax, which usually lies in a longitudinal groove in the mesosternum, is withdrawn,

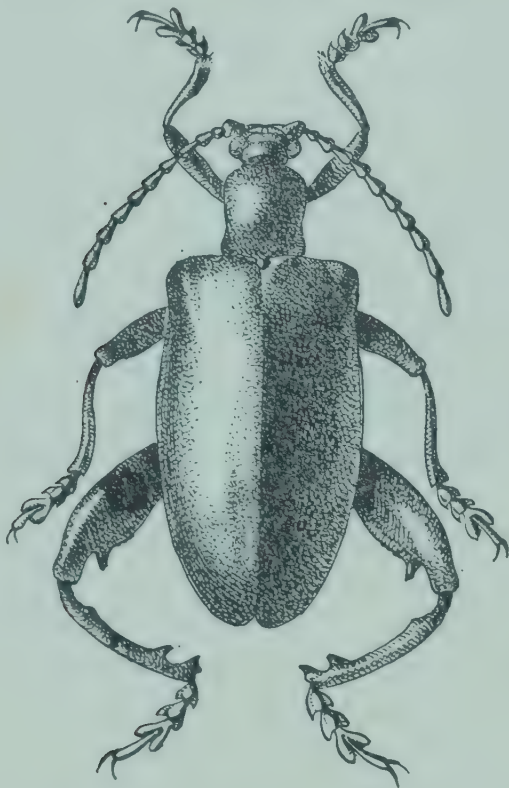


Fig. 88 – *Sagra femorata*, subsp. *empyrea* (Coleoptera: Chrysomelidae).

and then slammed back into its groove with an abrupt movement. Fig. 89. This produces a loud, sharp click, and the insect somersaults in the air. The process is repeated as often as is necessary, until the beetle lands right way up.

Digging. A great many insects live in the ground, in such a way that

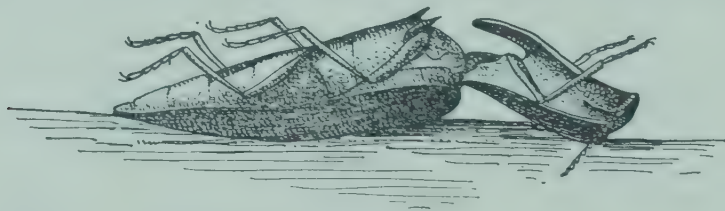


Fig. 89 – An Elaterid (click-beetle) lying on its back, at the moment that it is about to spring up. By suddenly flexing the prothorax, the process of the prosternum is made to strike against the mesosternum, and the insect is thrown into the air.

their main occupation is excavating the soil, and using for this purpose, sometimes the head, sometimes the legs, either of which may be specially modified for the purpose.

Digging is governed by a series of reflexes, which have been studied

experimentally. In SCARABEIDAE, for instance, Comignan has shown that when the epistoma touches a solid object the insect stops, with its head lowered, and its prothorax bent. If the surrounding temperature is low the beetle may remain still for a long time; above a certain temperature level the digging reflex is set off. In all fossorial insects we find that the digging reflex is linked with tactile stimuli in the head, with or without an associated temperature factor.

In sand-dune areas of the desert, high temperatures bring about digging. Sand-living beetles of the Sahara (*Heteracantha*, *Pimelia*, *Sternodes*, *Prionothea*) have the feet fringed with long hairs, which help to move the sand (Fig. 90). The insect works with each side of its body in turn: lying on one side it kicks vigorously with the three legs of the opposite side, throwing the sand backwards; then it leans on the other side, and does the same with the other three legs.

Swimming. In aquatic insects the legs are very variously adapted for swimming. All the phytophagous ones, and most of the carnivorous ones

Fig. 90 – *Sternodes caspicus*
(Coleoptera; Tenebrionidae)
(after PAULIAN). A desert
species, with fossorial
hind-legs.



walk on the bottom, or on submerged vegetation, using their legs as if they were on dry land.

Dragonfly larvae normally walk about looking for their prey, but if they are alarmed they can dart through the water by expelling water from the rectum. Those insects that are poor swimmers, like *Hygrobia*, may

use their legs alternately, but the expert swimmers—DYTISCIDAE, NOTONECIDAE, CORIXIDAE—have the two legs of a pair synchronized, like miniature wings.

Active swimming movements are needed for moving quickly through the water, and for diving to the bottom; an aquatic insect can generally come up again without effort, because the air-reservoir carried makes the body much lighter than water. Other organs besides the legs may be used for swimming. The tiny Hymenoptera of the genus *Prestwichia* use their wings, and mosquito larvae move by contortions of the body.

Flight. The mechanism of flight has been studied by cinematography, mainly in Diptera and Odonata. It must be said that there is a great variety of flight-mechanisms, and it is not possible to go into them at length here.¹

The speed of flight of various insects has been measured. The fastest are the Sphingid moths, with a speed of 50 feet per second (34 miles per hour), and dragonflies and horseflies, which achieve 46 feet per second. The slowest are undoubtedly the CHRYSOPIDAE and certain Chrysomelid beetles, such as *Agelastica alni*, which does not exceed 20 inches per second (1.12 miles per hour).

Insects with a strong flight sometimes migrate *en masse*. In tropical countries the locusts are only too well known to cover tremendous distances, sometimes being seen over 1,000 miles out to sea from the African coast. In all the climatic zones flights of butterflies and dragonflies have been recorded. The North American butterfly *Danaus archippus* sometimes moves in uncountable numbers across the Pacific or the Atlantic, and by this means has colonized Australia and Oceania on the one hand, and the Canary Isles on the other. It is claimed that these butterflies can rest on the surface of the sea, and then take up again their interrupted migration.

Beetles, although their flight is heavy, can still cover great distances. Turner caught the big Buprestid, *Chrysochroa ocellata*, in flight 250 miles from the coast of Bengal.

MEANS OF ATTACK

Active pursuit. Carnivores pursue their prey, some on the ground, and some in the air. The dragonflies take their prey in flight, and with their fore-legs extending forwards they are able to bring the victim to their mouth and eat it in the air. Many tropical Reduviid bugs keep watch at the tips of twigs, and pounce in flight on the flies upon which they feed; Asilid flies in turn do the same to many other insects.

On the ground predatory beetles, CARABIDAE or STAPHYLINIDAE, go after their prey, as it passes near, with mandibles open and antennae

¹MAGNAN, *Le Vol des Insectes*, 86pp., Hermann, Paris.

erect. Most of them see little unless it is moving; they hurl themselves at anything that moves, and bite as soon as their antennae have made contact with the prey. Others are attracted by smell, and here again the antennae play a leading part in their behaviour.

Thus the guiding organs of carnivorous insects are the antennae equipped with sensitive hairs, and other numerous and delicate sensory organs, and the insect must keep these in good condition, by ceaselessly combing them with special grooming organs situated on the fore-legs. These consist of rows of spines in rows like the teeth of a comb, sometimes on the fore-tibiae (Carabid beetles), sometimes on the tarsi (Hymenoptera), sometimes fashioned from the tibial spurs (ants) Fig. 91.

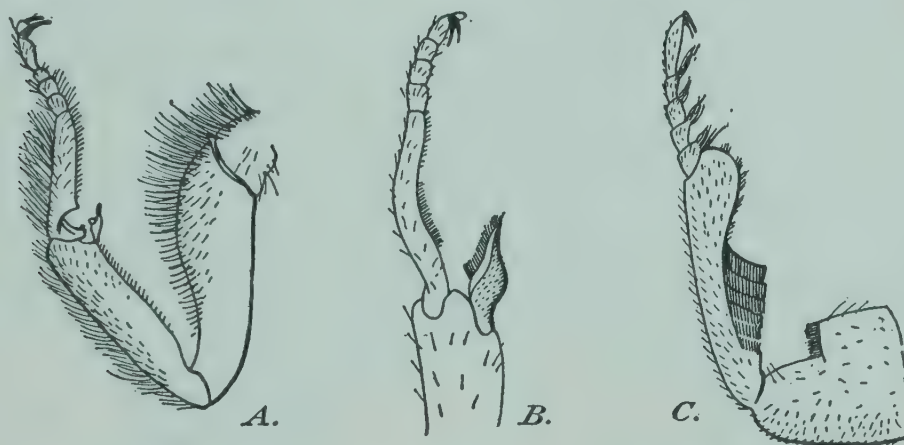


Fig. 91 - Different types of modification of the legs for grooming purposes. A, *Apis mellifica* (Hymenoptera); B, *Myrmica rubra* (Hymenoptera); C, *Lathrobium brunnipes* (Coleoptera).

If many predators take their prey by pursuit, others lie in wait for it. These remain motionless in a place where their chosen game is likely to occur, and very often they have some means of reaching out suddenly and taking their prey by surprise. Some keep their mandibles wide open in readiness. Dragonfly larvae in water, and the small Staphylinids of the genus *Stenus* on land, have the labium very long and jointed, folded away when at rest, but capable of being suddenly shot out forwards to seize a victim. There are many predatory insects with raptorial fore-legs, in which either the tibia closes against the femur, as in the Mantids (Fig. 92) and Reduviids, or the tarsus against the tibia (HENICOCEPHALIDAE).

Many predatory insects inject into the tissues of their prey a quantity of salivary juice, which kills it and starts the process of digestion. In Reduviids this salivary fluid is alternately injected and sucked back by a complicated organ at the base of the rostrum (*see above*, Fig. 61).

Predatory insects attack other adult insects in preference to larvae, but they often attack worms or Mollusca. Those which prey upon molluscs may be specially modified. For example, many malacophagous beetles

have the fore part of the body modified in a way that is called *cychrization*: the head is protractile, the mandibles elongate, and the prothorax strongly drawn forward. This deformation is the rule in the genus *Cychrus*, and is found in many other snail-feeders, CARABIDAE (Fig. 93), and Silphids. When the beetle has bitten its victim, and the snail has retracted into its shell, the modified body of the beetle allows it to retain its hold by the mandibles, while letting itself be drawn into the shell.



Fig. 92 – *Mantis religiosa* (Orthoptera: Mantidae), lying in wait for a victim, its raptorial legs folded in readiness.

Traps. Predators often make use of traps. In sandy areas *Scarites*, *Broscus* and certain *Staphylinus* take their prey to the bottom of pits which serve the beetles as a hiding-place during the day and a feeding-place at night. Cicindelid larvae lie in wait in the opening of a vertical pit, with only their cephalo-thoracic disc protruding. Ant-lions (MYRMELEONIDAE) and Worm-lions (*Vermileo*, Diptera, RHAGIONIDAE) make traps in the form of conical pits, and knock down with a jet of sand any insects that venture on to the slippery sides.

Other varieties of traps are employed by different groups of insects.

DEFENSIVE MECHANISMS

Piercing organs. Many insects that are spoken of as 'biting', or 'stinging' use either the rostrum or an abdominal sting built up from the

female genital armature, to defend themselves by injecting a toxic liquid into their enemy. The pain of the sting puts the aggressor to flight.

Not all insects that have piercing mouthparts use them as a defence. The bloodsucking Diptera (mosquitoes, TABANIDAE, *Stomoxys*) use their mouthparts only to get food. Hemiptera, however, will bite if they are picked up, and most entomologists have suffered the shooting pain of a bite from a Reduviid, a Notonectid, or a Corixid.

In contrast, the abdominal stings of female Hymenoptera are always a weapon. Wasps and bees pounce upon their enemies and sting them.

Other kinds of defensive weapons are found in some insects, notably the possession of urticating hairs, as in processionary caterpillars.

Defensive secretions. Strongly smelling secretions of glands in the integument often play a part in defence, and special glands may be developed for the purpose. The best known of these are the pygidial glands (anal glands) of Carabid beetles.

Almost all CARABIDAE, but above all those which were formerly grouped together as Truncatipennia, possess a well-developed pair of anal glands. BRACHINIDAE, PAUSSIDAE and OZENIDEA follow the same pattern, in that the liquid secreted is spread over a perforated disc, and is then projected with a sharp sound, producing a caustic cloud. The caustic

Fig. 93 – Cychrization of *Macrothorax aumonti* (a Carabid beetle) from Morocco. The elongation of the head and pronotum allows the Carabid to prey upon snails, see text.



constituents in the cloud include formic acid in CARABIDAE and iodine in PAUSSIDAE.

These 'explosive glands' of the BRACHINIDAE are undoubtedly powerful defensive weapons against small enemies, but they are far from giving complete protection to the beetle. This is true of all defensive weapons, whatever they may be. Paulian states that in the Cameroons monkeys

(*Papio*) look for the big BRACHINIDAE as delicacies, while scorpions (*Buthus occitanus*) attack with impunity, and devour, the *Aptinus displosor* that lives alongside them.

Glands of a remarkable kind are the *evertible glands* of certain beetles (Fig. 94). These are tubular, and under the pressure of blood they turn inside-out like a glove-finger, projecting their secretions outside the body.

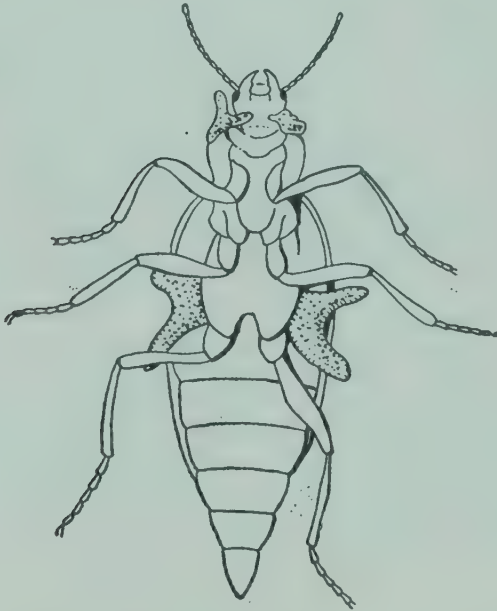


Fig. 94 – Evertible glands in *Malachius bipustulatus* (Coleoptera) (after KLEMENSIEWICZ).

Undoubtedly these are defensive organs, but their secretions are odourless to man. When *Staphylinus* and *Stenus* take up an attitude of defence they evert a pair of glands at the tip of the abdomen, and *Malachius* can make two enormous bright red glands emerge from the membranes between both the head and thorax and the pro- and meso-thorax, respectively, with a secretion that is very fluid, but odourless.

Reflex bleeding (Fig. 75). This is another defensive mechanism, in which an insect can make drops of its blood ooze out through the inter-segmental membranes. This happens in species whose blood is toxic, notably COCCINELLIDAE, CHRYSOMELIDAE (*Timarcha*), MELOIDAE and CANTHARIDAE.

A distinction has been drawn between *autohaemorrhoea*, in which only drops of pure blood are expelled in this way, and *autohaemaphrorrhoea*, in which the secretion is a foamy mixture of blood and air. Blood is expelled particularly through the joint between the femora and tibiae, at a time when the insect is feigning death, in reflex immobility, with the legs folded on top of the body. In some cases the internal pressure of the blood ruptures the intersegmental membrane, but in COCCINELLIDAE, *Meloë*, and *Timarcha* a pre-existing vent opens. It has been suggested that this vent is a modified gland in the articulating membrane.

All these glandular secretions, or evacuations of blood have the property of making the outside of the insect unpleasant to taste. The principal enemies of insects, birds, learns by experience, as a result, to recognize those species that have a disagreeable taste, and to avoid them. We shall see later on how this fact has been used by exponents of Darwinian evolution to explain the origin of warning coloration.

Shields, and attitudes of defence. Sometimes the chitin of the integument may become so hard and thick that it is proof against every attack. *Brachycerus* (CURCULIONIDAE) and certain Buprestids are so thick that they can resist the beaks of birds. For good measure the mouthparts are protected by a *mentonnière*, or chin-piece formed from the prosternum, and the antennae and legs are so hidden in their grooves that they are immune from damage. The very shape of the body is a protection, since many of them can roll into a ball, leaving a perfectly smooth surface upon which mandibles can make no impression.

On the same lines we may look upon the 'spectral attitude', well known in Mantids (Fig. 95) and common among Orthoptera. Opening its wings

Fig. 95 – A Mantid in its defensive attitude, which is known as the 'spectral attitude' (after CHOPARD).



in a threatening attitude, and spreading out in full view an array of bright colours, the insect is supposed to be able to frighten an attacker and put it to flight. This mundane explanation of the spectral attitude should be received with reserve. When attacked by a bird, the butterfly *Caligo* is

supposed to frighten its aggressor by lowering its head and exposing the underside of its wings, which look like a bird-of-prey. Geometrid caterpillars erect themselves, and sway about to look like snakes (Fig. 96).

All these interpretations are strongly tinged with anthropomorphism.

Reflex immobility. This, on the contrary, is a phenomenon that is



Fig. 96 – Caterpillar of *Leucorrhampha ornata* (a Sphingid moth from Brazil) in its defensive attitude (after MILES MOSS). The posterior part of the body imitates the head of a snake.

well established. A frightened insect lets itself fall to the ground and feigns death. This should not be confused with the accidental fall of an insect that is fleeing desperately from an enemy: only insects that cannot fly away or otherwise take to flight will feign death. It is commonest among beetles, but may be seen also in stick insects (*Carausius*), and in some wingless Diptera.

In the Kerguelen Islands, *Calycopteryx moseleyi* (Diptera, MICROPEZIDAE) is wingless and is found on the leaves of the Kerguelen cabbage (*Pringlea*), of which it sucks the exuding juices. As one comes near to the plant the flies can be seen to stop, fold their legs, and let themselves fall down into the deep cleft of the leaf-axils of the *Pringlea*.

This falling action of *Calycopteryx* on the leaf of *Pringlea*, like that of the weevils on its branch, is not quite identical with reflex immobility, as it has been studied experimentally on many insects. It is known that certain local tactile stimuli bring about partial or total immobility in many insects, and that there are also certain areas (called *dynamogenous*

areas) where a touch can cancel the immobility. We are concerned here with simple reflexes, and Rabaud has even shown that this experimental reflex immobility does not involve the cerebral ganglia.

Reflex falling of an insect from a leaf is in quite a different category. The fall of *Calycopteryx* is not brought about by a simple tactile stimulus. The leaves of *Pringlea* are continuously swayed by the wind, without these vibrations having the least effect on the insect; yet the reflex fall takes place at the slightest touch of a hand, scarcely brushing the leaf, or even to a shadow suddenly falling on the insect. So Rabaud says that the falling of such insects is not a simple reflex, but involves a certain degree of co-ordinated behaviour. It is a flight reflex, like that of the tree-living Cicindelid *Pogonostoma* in Madagascar, which moves round to the other side of the branch and hides from the sight of an enemy. In both these cases visual as well as tactile stimuli are involved, and we cannot then say that the cerebral ganglia do not play a part.

Shedding and regeneration of limbs. Although reflex shedding of limbs is much less widespread among insects than among Crustacea, it is quite common in Orthoptera. When an insect of this Order is trapped by one of its legs it is generally able to detach the limb spontaneously, in order to escape. The limb separates near the base, between the trochanter and the femur, where a suture is already present in insects, and there are special modifications which make amputation easy, and arrest the flow of blood. Phasmida have a ring of chitin at this point, so that the division of the limb can take place without either severing muscles or losing blood.

The spontaneous shedding of a limb is called *autotomy*. Orthoptera TETTIGONIIDAE have a special form of autotomy—a *Barbitistes*, for example, will turn round and bite off the trapped limb with one sharp nip of its mandibles—and this is called *autopsalism*. The ability to shed limbs occurs sporadically, and may be present or not in closely related species. Phasmida of the genus *Bacillus* shed their limbs very readily; *Carausius* do not.

Autotomy obviously has an immediate value in an emergency, but it leaves the insect handicapped for the future. In a great many insects this can be overcome by regeneration of the lost limb, which takes place as a matter of course if the accident occurs during one of the larval instars; the limb reappears intact at the next moult. Many hemimetabolous insects can regenerate limbs, even if they have not got the power of autotomy.

The general rule about regeneration is that the nearer to the tip the limb is severed, the easier it is to replace. The regeneration of a tarsus is easy: that of a whole limb is much more uncertain. The sequence of events is as follows. As a start the wound forms a scar of amoebocytes, underneath which cells of an embryonic appearance come into being in contact

with each of the different kinds of tissue involved. The regenerated member is then present in embryo, comes into being at the next moult, and grows bigger at each succeeding moult.

A regenerated limb is always less highly developed than the original one (Fig. 97), and is often incomplete: for example the regenerated tarsus of *Blatta* often has only four segments instead of five. Sometimes regenera-

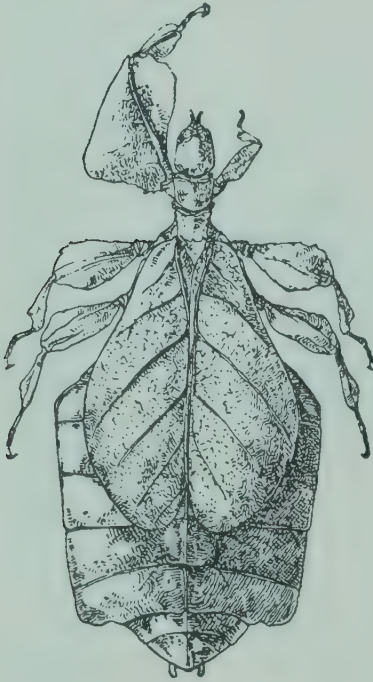


Fig. 97 – *Phyllium bioculatum* (Orthoptera; Phasmidae); a female, showing regeneration of the right fore-leg (after CHOPARD).

tion is heterotypic, that is to say it gives rise to an appendage of a different type from that which was lost. This may be an appendage from a different part of the body (*heteromorphosis* of Loeb, *homeosis* of Bateson). If we cut off the antenna of a Phasmid in the region of one of the first few segments, under certain conditions the limb may grow again as a leg instead of an antenna. In *Blatta* it is possible to get an antenna in place of an eye.

Natural and artificial shelter and camouflage. The great majority of insects seek shelter, either of a permanent or a temporary kind, and a large number of them hide under stones, in cracks in the ground, in dead wood, or under bark. We have already noted how the thigmotactic reflex, which leads insects to press their body-surface against a solid object, plays an important part in this instinct for concealment. Other insects, not content with making use of natural shelter, build one of their own.

Dragonfly larvae, and those of *Reduvius personatus*, clothe themselves in a covering of fragments of debris to disguise their appearance, and so practise a true camouflage. Among Coleoptera, the larvae of CASSIDAE and those of *Crioceris* (CHRY SOMELIDAE) have the anal extremity of the

body bent forward so that it overhangs the dorsal surface, and supports a hood composed either of excreta (*Crioceris*), or of the empty skins of previous instars, which are cemented together with dung. In Southern Ethiopia the larva of an *Acanthaspis* (REDUVIIDAE), living under bark and feeding upon ants, piles up upon its back the skins of the ants that it has sucked dry. When the bark of a dead tree is lifted up there is a scurrying in all directions of little heaps of agglutinated ant-skins, ranging in size from that of a pea to that of a small nut, each borne on the back of a very active bug.

Using a more perfect technique, other insects build themselves chambers from a variety of materials, which are held together with saliva, dung or silk. In running streams the larvae of Trichoptera (caddis-flies) live in cases, the form and structure of which can be used to identify the species. The legs are held forward, outside the case, which the insect keeps in repair by the use of its hooklike urogomphs.

Among terrestrial insects the caterpillars of the Lepidopterous family PSYCHIDAE build portable cases similar to those of the caddis-flies. Some beetle larvae, such as *Clytra* (CHRYSOMELIDAE) live in cases which they carry like a snail's shell, and into which they can retreat, closing the orifice with their head, which is strongly chitinized.

Silk is much used by insects for building shelters. It is generally secreted by glands opening on the pharynx, but silk glands have been found to occur in all the other parts of the body. The larvae of *Hemerobius* (Neuroptera) and of certain *Lebia* (Coleoptera) secrete silk by their Malpighian tubules, and pass it out of the anus. *Embia* (Embioptera) make silk in their fore-tarsi, which are dilated like hands, and use it to build nests under stones.

MIMICRY AND PROTECTIVE COLORATION

Here again we are dealing with a defence-mechanism that is not a guarantee of safety, but which undoubtedly has value. These devices in insects are so interesting that they deserve a separate section each.

Cryptic coloration and shape (Pls. 2, III, IV, V). Cryptic coloration exists when the animal resembles its surroundings (*homochromism*). Very often there is a resemblance to the shapes, as well as the colouring of surrounding objects and this is generally called *homotypism*, but I prefer to call the resemblance of shape *homomorphism*, using the term '*homotypism*' to cover both phenomena. This cryptic resemblance to inanimate surroundings must be distinguished from *mimicry*, which is a resemblance to another animal.

In all open situations there are many animals with a colouring more or less that of their surroundings. In a desert many animals of all groups are tawny; in a forest many birds, reptiles and insects are green. Most

often this simple homochromism applies merely to the colour of the skin, but in many insects the protective resemblance is improved by the choice of a place of similar colour in which to sit, or by taking up a deceptive attitude, or even by covering the body with a screen of debris.

The homotypic animal, as we have seen, has the shape as well as the

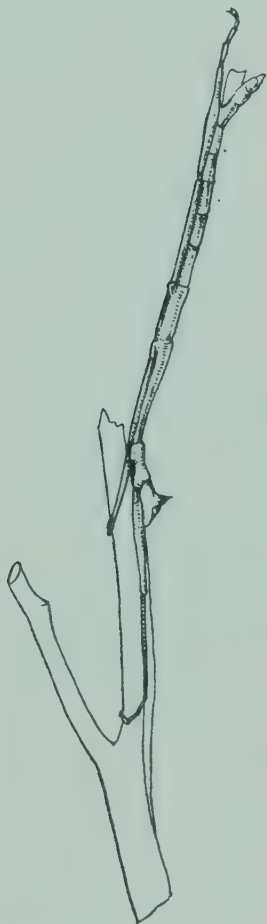


Fig. 98 – *Parasosibia parva* (Orthoptera; Phasmidae) in a resting position alongside a branch (after CAPPE DE BAILLON).

colour of its surrounding, and it may add to the effect by remaining immobile in a particular attitude (Fig. 98). Everybody knows how the Phasmids look like bits of dead stick, Pl. 2, IV (1), and the leaf-insects look like leaves, Pl. 2, III (1, 2). Some Orthoptera of the Sahara Desert have a flattened body with a rough surface which, in conjunction with its colour, makes them look just like stones. Pl. 2, V (3).

Some insects look just like the bark on which they live. Examples are found among Orthoptera, Pl. 2, IV (2, 3), Coleoptera, Hemiptera (*Phloea*) and Lepidoptera, Pl. 2, V (1, 2). Others occur on flowers, and take up the same colouring, as in certain tropical Mantids (*Gongylus*, *Hymenopus*). The pose and the immobility of these insects makes them difficult to see (Fig. 99). Many Orthoptera that live on foliage have more or less the appearance of leaves, and those Mantids that have big thoracic expansions, or those butterflies that have the wings naturally notched and serrated,

can easily be mistaken for dead leaves. The leaf-insect *Phyllium* has brought to perfection the cryptic resemblance to a leaf, with abdomen spread out, the legs leaf-like, and the elytra clearly marked with the veins of a leaf. Pl. 2, III (1). As a final touch, *Phyllium* lays eggs that look just like seeds.

Amazing as is the protective resemblance of the PHYLLIDAE, or 'walking leaves', there are some insects that are even more extraordinary. The oriental Lepidoptera of the genus *Kallima* (*Frontispiece*) have vivid colours on the upper surface of the wings, but the under surface is brown. They prefer to rest on the branches of certain shrubs, where their attitude, with the wings held up and pressed together over the body, together with the shape and colour of the under surface, makes it almost impossible to distinguish them from dead leaves. The pattern of the under surface



Fig. 99 – Caterpillar of *Selenia tetralunaria* (Lepidoptera) disguising itself as a twig of a pear-tree (after WEISSMANN). A tubercle on the dorsal surface of the body imitates the scar where another twig has broken off.

imitates veins, the 'tails' look like leaf-stems, and little yellow and black spots on the wings look like the moulds and rusts common on dead leaves. This sort of thing is pushed to an extreme in certain grasshoppers

(Fig. 100), where tiny spots of colour imitate not only fungal growths, but also the mines of phytophagous insects.

Examples of protective coloration in insects could be multiplied indefinitely. H. B. Cott has analysed the various types, and arranges them in four groups, as follows:

1. Homochromism in the strict sense, that is, having acquired the colouring of the substratum.



Fig. 100 – *Pycnopalpa bicordata* (Orthoptera) (after CHOPARD). A cryptically coloured long-horned grasshopper, the wings of which have spots that look like patches of fungus on a leaf.

2. Disruptive coloration, or a camouflage: contrasting patterns are superimposed so as to distract the eye, and prevent it from recognizing the natural outlines.

3. The elimination of shadows, by flattening the body, and blurring the contours.

4. The elimination of shadows by taking up an attitude which disguises the relief of the insect, as in Fig. 101.

Alongside the permanent cryptic resemblances that we have considered already may be set the changeable patterns found in reptiles and fish, where the animal does not seek out a place of a suitable colour; instead it changes its colour, and even its shape, to harmonize with the surroundings in which it happens to be. In the chameleon, for example, it is known that the colour-changes are brought about by modification of the chromatophores, pigmented cells in the integument, mobile and contractile, and in a variety of colours. The changes produced in these cells by the action of the sympathetic nervous system are controlled by the eyes. If an eye is covered up, or a section of the sympathetic nervous system damaged, then the corresponding area of skin ceases to change colour.

There is no doubt, therefore, that reflex colour-changes in the skin are

brought into play by the action upon the eye of the light reflected from the surroundings. The animal automatically reproduces upon its skin the general impression of colour and contrast that is received by its eyes.

The same sort of thing is known in insects. Phasmida, and especially *Carausius*, *Bacillus* and *Donusa* have a chromatic rhythm by which their coloration is paler by day than by night. This rhythm depends on the movements of pigmented granules, green, yellow or dark brown, inside the hypodermal cells, which in this way become true chromatophores, if not very specialized ones (Fig. 102). It is agreed that this chromatic rhythm is controlled by a reflex originating in the eyes, the effect of which is to liberate into the blood hormones which are responsible for the pigmentary changes in the hypodermal cells.

Mechanism and purpose of cryptic coloration. Darwin and Wallace were the first to insist that homochromism was a protective device, but although it seemed obvious that there must be some truth in it, a great deal of dispute has arisen subsequently. Supporters and opponents of natural selection have been determined to demonstrate either that protective resemblance was effective in the struggle for existence, or that its value was negligible.



Fig. 101 – Caterpillar of *Smerinthus* (Lepidoptera; Sphingidae) (after COTT). Concealment by the use of shading: the caterpillar on the left is less conspicuous because it is clinging upside down, presenting its darker under-surface to the light.

It is obvious that it cannot be claimed that cryptic coloration gives complete protection. No doubt, at least in certain cases, this is one of a number of methods of defence, along with armouring of the integument, spines, and attitudes of concealment, all of which tend to insulate the individual against the hostility of the outside world. They never protect the individual completely, and many casualties occur, but for the species

as a whole these devices have a relative value in the struggle for existence, and the balance between one species and the others.

Darwin and Wallace accounted for the origin of homochromisms by natural selection, but it has been pointed out long ago that selection could only perfect something that was already there, and could not bring it into being. In fact, a simple reaction of organisms to light may explain the origin of protective colouring. Some of the pigments concerned are simply ingested with the food of the animal, and accumulated in the tissues. This nutritional homochromism can be seen in phytophagous

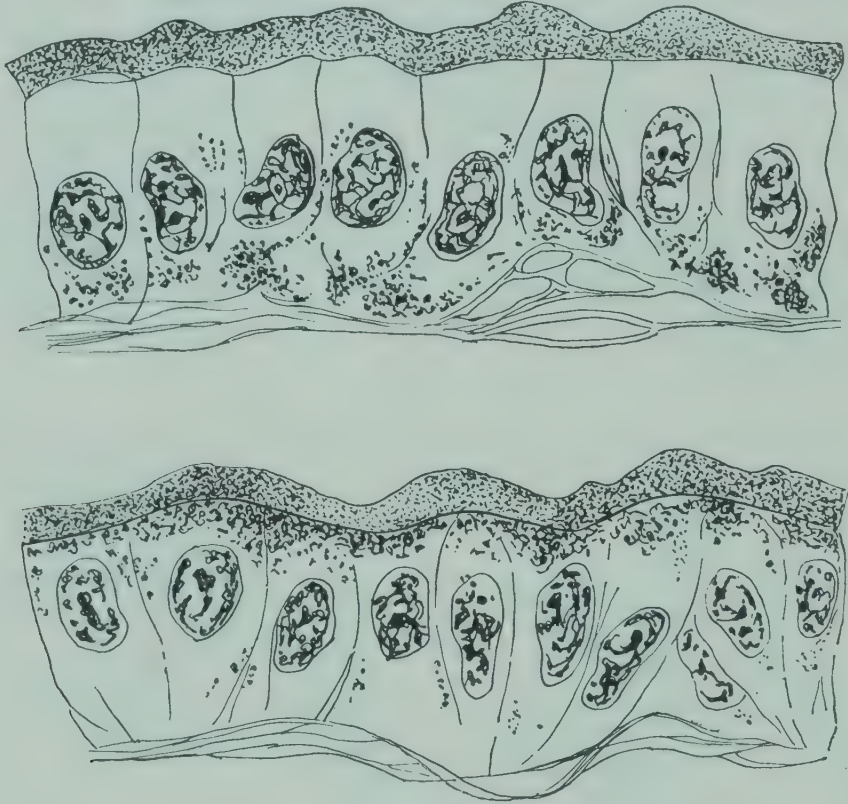


Fig. 102 – A chromatic rhythm in *Carausius*, brought about by migration of the pigmented granules in the hypodermal cells (after JANDA). Above, diurnal position, giving the insect a pale appearance; below, nocturnal position, making the insect dark.

insects and in parasites. The green colour of Phasmids and of Phyllids is caused by taking in chlorophyll. There is a connexion between nutrition and the formation of the lipochromes that are seen in insects. The larvae of the Homopteran *Eurycorypha*, feeding upon the petals of red roses, take on a red tint.

Apart from these cases where pigment is directly derived from food, the coloration of cryptically coloured insects is independent of diet. The formation of pigments, and probably also of structural (interference) colours comes about by an action of the light in a way rather like that of the chameleon, except that the effect that we are studying concerns a

species instead of an individual. The chameleon, during its lifetime, reproduces on its skin the effect of colour and pattern that its eyes see around it. All animals do this, but on a different time-scale, not during the lifetime of a single individual, but in the course of evolution of a species.

We can see without difficulty that, in an insect which spends most of its life stationary on the ground, on a tree-trunk, or on foliage, the light reflected from its surroundings is continuously at work upon the eye, bringing about a visual reflex, and affecting the colour and pattern of the body pigments. It is a fact that not all Lepidoptera expose the same surface of their wings to the light when they are at rest. It is always the surface that is exposed by the resting insect that develops cryptic coloration: the under surface in butterflies, the upper surface of the fore-wings in moths. Pl. 2, V (2).

The determination of colour is not the only effect of this reaction of organisms to light. The same mechanism influences shape. Visual reflexes of the same kind have brought into being a series of behaviour patterns—disguise, choice of a support, or a pose to take up on it—all related to, and used in conjunction with, cryptic coloration.

But, we might say, if this is so, should not all animals be cryptically coloured? Not at all. Many other adaptations counteract the tendency to develop cryptic coloration. Homochromism proceeds only in sedentary animals, and even among them it affects only those which live in brightly lighted places, and which are diurnal.

Must we postulate a selection of the most useful variations, in order to explain why resemblances have become so perfect? It seems not. Sometimes the resemblance is so minute that it is hard to see what selective value there could be in the finer details. Of what use can it be to *Kallima* to suggest the attacks of parasites by details so small that they can be seen only with a magnifying-glass? This perfection of detail is a useless embellishment. On the other hand we can understand how this comes about if the protective resemblance is merely an impressionist copy of its surroundings on the insect's skin. The fixing of the mechanism in the course of countless generations, and the accumulation in the hereditary material of the acquired modifications, all tending in the same direction, makes the process of mimicry go on without limit, and produce a *hypertely*, that is an evolution going far beyond what is any longer useful to the insect.

Naturally, such an explanation of the origin of protective resemblance implies that variations acquired during the life of an individual can be inherited, somehow or other.

Warning colours. As a contrast to the cryptic, or homochromic colours there are gaudy warning, or *aposematic* patterns. According to Wallace, certain animals that are already protected in some way, either by defensive

weapons, or by having an unpleasant smell, or by not being edible, have developed in addition conspicuous markings which give warning to would-be predators. The latter find out what is unsuitable as food by experience in their young days, and learn to avoid animals having this warning coloration.

In fact, the practical value of these alleged warning colours has never been clearly demonstrated. Observers have let their imagination run riot, sometimes to a laughable extent, as in the so-called defensive attitude of



Fig. 103 – Three small cockroaches of the genus *Prosoplecta* mimicking ladybirds.

Caligo and the spectral pose of Mantids, to which we have already referred.

Mimicry (Pl. 2, VI). This is the resemblance, at times very superficial, that certain species of animal bear to other animals which live in the same habitat. As a result, the ‘mimic’ comes to have an appearance different from others of its own group. Innumerable examples of mimicry have been claimed, but not always convincingly. We must rule out all the false, though at times ingenious, comparisons that have been made between quite different animals that have accidental points of resemblance, and confine ourselves to those which satisfy the conditions laid down by Wallace:

1. That the details in which the mimic copies the model are all striking ones: in minor and inconspicuous details it remains true to its own group. For example, *Aegeria apiformis* is a moth which looks like a Hornet, but the body is still covered with scales, and the antennae and proboscis are still those proper to Lepidoptera. Pl. 2, VI (1, 2).

2. The mimic should seem to benefit from its resemblance to the model: *Aegeria* is defenceless, the Hornet is aggressive and dangerous.

3. The mimic must be less common than the model. It is significant that many mimics imitate the social insects, bees, wasps and ants.

Categories of mimicry. Three general categories of mimicry can be recognized in insects.

Batesian mimicry (named after Bates) is that in which a vulnerable

species copies another that is unpalatable, or otherwise defended, and which has warning coloration. The pattern developed by the mimic is called a 'pseudaposematic' one, or a false warning coloration (Fig. 103).

Müllerian mimicry (named after Müller) occurs when two or more unpalatable or well-defended species have developed the same pattern of warning coloration, which is then called 'synaposematic'.

Finally, there is a third—*parasitic mimicry*—in which a parasite comes to resemble its host.

The commonest of the three types is Batesian mimicry, like that of the *Aegeria* and the Hornet, mentioned above. Many tropical butterflies that are defenceless imitate members of other families (DANAIDAE, HELICONIDAE, etc.) which are protected by having glands on the wings to produce an unpleasant secretion, making them distasteful to birds. One of the best-known examples of this is *Papilio dardanus*, distributed throughout tropical Africa. Pl. 2, VI (3–7). In this species there are more than forty different forms of the female, all of restricted distribution, some with a pattern akin to that of the male, others totally different, and imitating instead a species of Danaid that is found in their immediate locality. In every part of Africa the female of *Papilio dardanus* mimics the local Danaid, not only in colour and pattern, but also in its attitude and in its flight.

Müllerian mimicry is less common than Batesian. Here the mimic and its model are equally well-protected in other ways, and it is not obvious at first sight what benefit they can derive from resembling each other. The many species of wasps have the same striking pattern and colour; and in the same areas of South America occur the two families of butterflies, DANAIDAE and HELICONIDAE, both of which are already unpalatable, yet they, too, have the same pattern as each other.

As for parasitic mimicry, it is well known that many commensals and parasites resemble their hosts. The flies (*Volucella*) whose larvae inhabit the nests of Hymenoptera, themselves as adults mimic the drone of the nest in which they were reared. Here, too, we may mention the ant-like appearance of many insects and Arachnids that live in ants' nests.

There is a lot to be said about parasitic mimicry. Some have alleged that the mimicry by *Volucella* enables the fly to come and go near the nest without attack, but can we really believe that the bees and wasps are so easily deceived. Besides, do we not know that social Hymenoptera show complete indifference to dangerous parasites. And again, what protection can result from the ant-like appearance of the myrmecophiles? These are completely guarded against enemies from outside the nest, and against the ants themselves we cannot imagine that the mimicry can be good enough to deceive.

An explanation of mimicry. In the first place let us get rid of the idea

that striking colour and pattern can really serve warning to insectivorous animals, and drive them away. This kind of fraud may deceive the imperfect observation of human beings, but surely it will not deceive the more acute vision of a bird.

If we examine the facts fairly, without begging the question, we realize that the practical value of mimicry is far from being proved. Besides, it is hard to see how natural selection could develop a mimetic resemblance, since the latter would not give any protection until the mimicry was almost complete. In fact, as we have shown above, cryptic coloration arises in sedentary species by the action and stimulus of light. Nomadic species are deprived of the effect of living in a constant environment, and have developed other means of protection, such as venomous and distasteful secretions. These insects, therefore, have never developed a cryptic coloration, and they remain highly coloured and strikingly patterned.

The colour and pattern of non-sedentary species may not have developed along cryptic lines, but they follow certain rules, nevertheless. It can easily be confirmed that the boldly patterned diurnal butterflies of each of the zoogeographical regions have certain elements of colour and pattern in common. So much so that a lepidopterist without much difficulty can look at a butterfly and say which region it probably came from. There is no doubt that the local environment has a direct effect on colour and pattern, and much Müllerian mimicry can be simply explained as convergence.

Thus we may say that each zoogeographical region has its own palette of colours. The butterflies of South America are very often red and black, but this combination of colours is never found in Africa, nor in India, where the combinations are black and green, and black and blue respectively. In the Pacific combinations of yellow and pale green, or yellow and pale blue predominate. The aposematic pattern of yellow and black occurs in a multitude of diurnal Lepidoptera of a variety of groups: in Africa the yellow merges into a tawny red, and in America into orange.

The wing-pattern of insects in its primitive form consisted of longitudinal bands, and evolution took place by breaking up of the bands, and union of the fragments into transverse bands. The same sort of evolution going on in different insect stocks has very often produced resemblances between them that have been credited to mimicry, whereas they are no more than convergences.

Biologists no longer believe that Batesian mimicry could have developed by the sole agency of natural selection of a succession of small variations, having first of all produced some vague resemblance to a well-protected species. The mutationists, too, labour under the disadvantage of having to maintain that genetic mutations, arising by

chance, could so often bring about resemblances between species to a degree of perfection that would have protective value immediately.

The truth is that the facts can be explained more naturally by invoking the Lamarckian principle of the inheritance of acquired characters. In the same way that the cryptic colorations are brought about by the reaction of living tissues to optical stimuli received through the eyes, so the aposematic patterns arise from complex actions of light under the same environmental conditions, but on different organisms. Cases of mimicry are caused by the way of life of the mimic, which is subjected to influences identical with those to which the model is exposed. The same causes produce the same effects, and mimetic resemblances are really no more than convergences.

PARASITISM

Parasitism plays a great part in the biology of insects. Etymologically speaking, a parasite does no more than live alongside another, but as used by biologists the word always implies that it does some injury, or in some way lives at the expense of its host. As Grassé has put it, the parasite draws upon another being, its host, for the normal, necessary, and direct supply of materials that it needs for its metabolism.

This definition separates the parasite from the predator, since the parasite does not cause the death of its host; it also separates the parasite from the commensal, which does no harm to its host. These differences are of degree only, because examples can be found of all the intermediate stages. Reduviid bugs catch other insects, and suck their blood in the same way that a mosquito sucks the blood of a mammal: the former is called a predator because it kills its victim, while the mosquito is called a parasite, yet the difference is not in the method of attack, but in the size of the victim.

The classification of parasites has been carried to excess, with a multiplicity of categories, which we cannot enumerate here. It will be enough to mention the principal classes of parasites.

Commensals. The commensal gets its food from its host, but painlessly to the latter, which may even benefit from the association. The Histerid beetle *Teretrius parasita* eats the droppings of the wood-boring beetle *Sinoxylon*, without harming the latter; indeed it renders a service to it by cleaning up after it. Very often the commensal is useful in such a way to its host, and these associations pass gradually, little by little, from commensalism into symbiosis.

Symbionts. Symbionts are species that are very different from each other, but one of which gives shelter to the other, the association having developed to such a point that neither can exist without the other. So in this case the symbiont takes something from the host, but the host cannot

do without it. The flagellate *Trichonympha* lives in the hind-gut of certain termites and is strictly dependent on its host, which in turn cannot digest cellulose, and will die of starvation if it is deprived of the *Trichonympha*.

Inquilines. We give the name *inquilines*, or *kleptoparasites*, to animals that live by stealing the food that some other animal has stored for its own use. There is every intermediate between harmless inquilines and true parasites. All degrees of kleptoparasitism have been observed, sometimes with remarkable habits, from the fly *Culicoides* piercing the abdomen of a mosquito and sucking the blood on which the mosquito has just fed, up to the solitary bee *Cerceris*, predator upon beetles, which drives out the bee *Trachusa* in order to occupy its burrow, and to the bee *Psithyrus* which kills the female *Bombus* in order to take possession of her nest, and to rear its own progeny there instead of hers.

In many cases of parasitism the parasitic insect is not modified at all, at any rate structurally, but when the parasitism has been long established adaptations may be evident. Each stage in the life-cycle of an insect tends to specialize in one phase of parasitism. The young larva may be adapted to the search for a suitable host, the older larva to exploiting it. In this way arise hypermetamorphosis and parasitic degeneration.

Endoparasites. Endoparasitism is rare in adult insects, but is the normal state of existence for the female Strepsiptera which live in the bodies of Hymenoptera and Homoptera. It is more usually a temporary phase in the larval life of an insect. This is true of TACHINIDAE (Diptera), of Microhymenoptera, which may exhibit polyembryony, or again of certain beetles, such as RHIPIPHORIDAE.

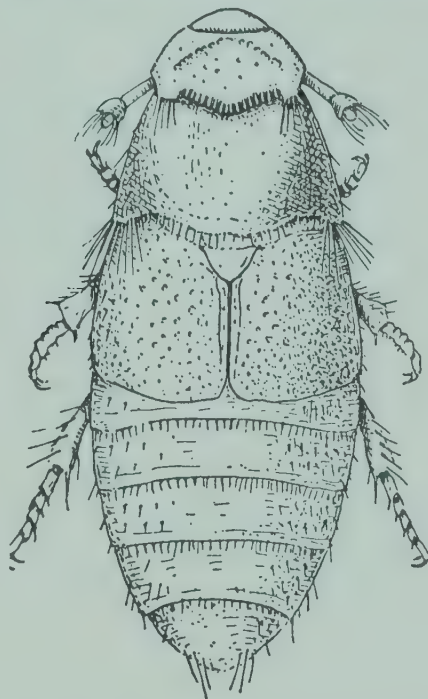
Ectoparasitism and phoresy. The greater number of parasitic insects are ectoparasites, that is to say that they live externally on their host, but it is difficult to draw a line between those that are true parasites, and those which are merely using the host for temporary transport, and so are practising *phoresy*. The small BORBORIDAE of the genus *Limosina* get themselves carried from one heap of dung to another by Scarabeid beetles. The cucujos, or fireflies of Central America carry large numbers of pseudoscorpions on their elytra. These arachnids are predators, and get the ELATERIDAE to carry them about over potential hunting-grounds. The triangulin larvae of MELOIDAE, hatching from the ground, climb on to flowers, and there attach themselves to the hairs of bees, which carry them to their nests.

Cases of phoresy also exist in mammals. According to Paulian, coprophagous SCARABEIDAE of the genus *Canthon* are carried, often in great numbers, in the fur near the anus of certain monkeys. *Leptinus testaceus*, which lives as a commensal in the nests of *Bombus*, is sometimes found in the fur of rats or of voles. This seems to be a case of phoresy, but other

LEPTINIDAE are known to be true parasites, *Leptinellus* and *Platypsyllus* (Fig. 104) on the Beaver, and *Silphopsyllus* on the Musk Rat.

Whole Orders of insects may be ectoparasites: Aphaniptera (fleas); Mallophaga and Anoplura (lice). So may whole groups of flies (Pupipara) and bugs (CIMICIDAE). Among Dermaptera *Hemimerus* lives on *Cricetomys gambiensis*, the African Giant Rat, or *Arixenia* on Indo-Malayan bats.

Fig. 104 – *Platypsyllua castoris*
(a Leptinid beetle), an
ectoparasite of beavers in
America and in Europe.



Among beetles the LEPTINIDAE (*Platypsyllus*) are often quoted as being ectoparasites, but there are others less well known. In South America Staphylinids are found in the fur of a variety of rodents and of opossums, living there in all their stages, and showing parasitic degeneration.

CONSCIOUS BEHAVIOUR

The psychology of insects has always provoked great argument among naturalists. We have the advantage of excellent observations collected together in turn by Réaumur, Fabre, and Ferton, and dealing with instincts, which are actually no more than the transformation into automatic actions of a kind of rudimentary consciousness. But alongside these instincts, which form a sort of species-memory, there is also in insects an individual memory, extensive and flexible, which plays a big part in behaviour. Its function has been brought to light, particularly in recent years, by experimental methods.

Conditioned reflexes. It was Pavlov who first had the idea of using conditioned reflexes to explore the consciousness of insects. For example, *Telea polyphemus* is a big Saturniid moth from China, nocturnal in habit, which spends the day immobile, hanging from a branch. It hardly

reacts at all to stimuli, but if it is gently manipulated between finger and thumb there is a slight response, chiefly a beating movement of the wings. If this is repeated a number of times, and each time a whistle is blown, there comes a time when the whistle alone will cause the wings to move, without touching the moth at all. A conditioned reflex has been induced.

The information that can be extracted from such an experiment is considerable. In the first place, it proves that the *Telea* must be able to hear a whistle, even though it does not show any reaction to it under normal conditions. Then, by varying the pitch and the loudness of the whistle, and using the conditioned reflex as a check reaction, we can explore the range that is audible to the insect. Techniques of this sort have been elaborated, using apparatus such as boxes offering a choice, or labyrinths offering alternative paths, and by these means experiments have been carried out that provide the basis for an experimental psychology of insects.

Drill. By inducing conditioned reflexes it is possible to teach a drill to insects, by which they continue to carry out some routine piece of behaviour. Kuhn and von Frisch were able to drill bees to associate the search for honey with certain colours. A big board was divided into squares painted in a variety of shades of grey, and honey was placed on one square, which was also marked with a spot of colour. The bees were thus conditioned to look for the honey where the colour was, and to disregard the grey background, or the position on the board. After this the colour alone would attract the bees, without any honey. As in the previous experiment, the way was now open for an exploration of the range of colour-vision of the bees. The experiment incidentally shows that colour-perception plays a part in the search for food by bees.

Other workers have used ants to see if insects had any sense of time. Grabensberger kept ants in artificial nests, and trained them to look for food at intervals of time ranging from three to twenty-four hours, or even longer. These insects must therefore be able to detect the passage of time with some precision. No doubt this mechanism is linked with their metabolism, because the time-scale of the trained bees varies with temperature. If the temperature is raised, the ants' metabolic clock gains, and if the temperature falls it loses.

Bees can be trained with equal ease to come and look for sugar outside the hive at fixed times, and it has been shown that sun-time plays no part in this. The bees' own memory alone is involved. Furthermore, it has been stated that this memory lasts hardly more than twenty-four hours, and may be destroyed sooner if some distraction occurs. For example, if trained bees are in the hive when a forager returns and performs a dance, they forget all about the sugar that is waiting for them, and go off on the hunt with the rest.

Labyrinths. Many experimental workers have made use of a labyrinth, or maze, more or less complicated, placed in front of a nest where ants were reared, in such a way that the ants were forced to go through it to reach their food. The study of the sort of errors that the ants make, and how they eliminate them by experience, gives valuable clues to the mental processes of these insects. Most experiments have been carried out on ants, but some, especially Turner and Allée have used cockroaches.

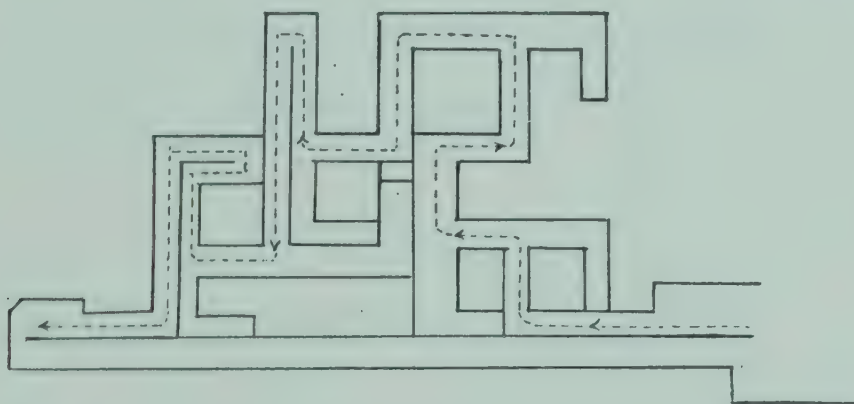


Fig. 105 – SCHNEIRLA's maze. The dotted line shows the path of an ant that succeeded in reaching the food from the nest, after the direct path has been closed.

Schneirla made use of a very complicated maze (Fig. 105), which he was able to make intelligible to *Formica incerta*. An experimental nest made of plaster was planned in such a way that it could only be supplied with food by worker ants that had found their way through the maze in both directions. At the start they were allowed to use a direct route, and hungry workers were released through it one by one, to reach a bait. Then a door was closed behind them, in such a way that they could get back to the nest only by going through the maze. After many attempts some of them succeeded in finding the way, and these were carefully segregated.

Thereafter these chosen workers, duly marked, were used for interesting experiments. On successive trials they progressively eliminated their own errors, and negotiated the maze more and more quickly. This learning took place more quickly for journeys towards the nest—that is in the direction of the original conditioning—than for outward journeys.

After an ant had learned its way through the maze perfectly, it became completely confused if the apparatus was turned to face a different way in relation to the light, thus showing that the insect's memory was not only for objects, but also for an orientation in respect of the sun. Temperature also had an effect. The period of learning was reduced to half if there was a brief lesson at 25°–30° C. instead of at 15°–20°C. On the

other hand, a perfectly trained ant lost all it had learned if it was kept for several hours at about 30° C.

Orientation and homing. In the study of the behaviour of bees and of ants, most attention has been given to their powers of orientation and observing their surroundings. It has been recorded a long time ago that young worker bees, when they leave the nest for the first time, fly backwards for a short while, and fix in their memory a picture of the nest and its surroundings. A visual memory is the principal means by which bees find their nest again. Just moving the nest a few yards away while the bees are absent is enough to confuse them completely, and they beat obstinately at the precise place where they last saw the entrance to the nest. In the course of successive flights the bees extend their knowledge of the surroundings of the nest.

An extensive study of these matters has been made in ants, and they have been found to use visual, olfactory or tactile guides, whichever was available. Their visual memory comprised not only an impression of objects and of their relative position, but also a sense of direction and of time, by which they were able to take account of their own movements, and of the change of angle between the sun's rays and the route they wished to follow. This can be demonstrated by various experiments.

Whenever a foraging ant finds something to eat she carries it back to the nest, *in a straight line*, working out its direction by the angle of the sun. Santschi has shown that the ant is completely confused if a mirror is brought near so that it reflects the image of the sun from a different direction. But even then, in due course the ant comes by chance upon some familiar object and finds its way back from that.

Pieron went on to make another experiment. When an ant had found some food, and was on the way back to the nest with it, he placed in its path a disc that could be rotated. If the disc was turned while the ant was on it, the latter had no difficulty in quickly finding the right direction again. If, on the other hand, the disc was moved bodily at right angles to the track, the ant now followed a path parallel to the original one, and stopped when it had gone the distance that ought to have brought it to the nest. Since the nest was not there, the ant had the greatest difficulty in finding where it was. Cornetz picked up the disc, with the ant on it, and carried it beyond the nest, and when it was put down the ant took up its original direction by the sun, and so moved directly away from the nest, leaving it behind.

Clearly a visual memory of objects is also brought into play to help the ant to find its route back. As noted by Turner, the ant makes a series of rapid twists and turns immediately outside the opening of the nest, which may be hard to see, and then no doubt it is taking note of points of reference. It has thus been demonstrated, by many experiments, that

ants, when finding their way back to the nest, rely mainly on visual aids, but their appreciation of distance is difficult to explain. A foraging ant has often come a very long way, by a tortuous route, before she finds her prey and returns to the nest. Experiment shows that in spite of this she still has a precise appreciation of the distance back in a straight line. It is very hard to believe that she can work this out from the muscular effort involved in the outward journey.

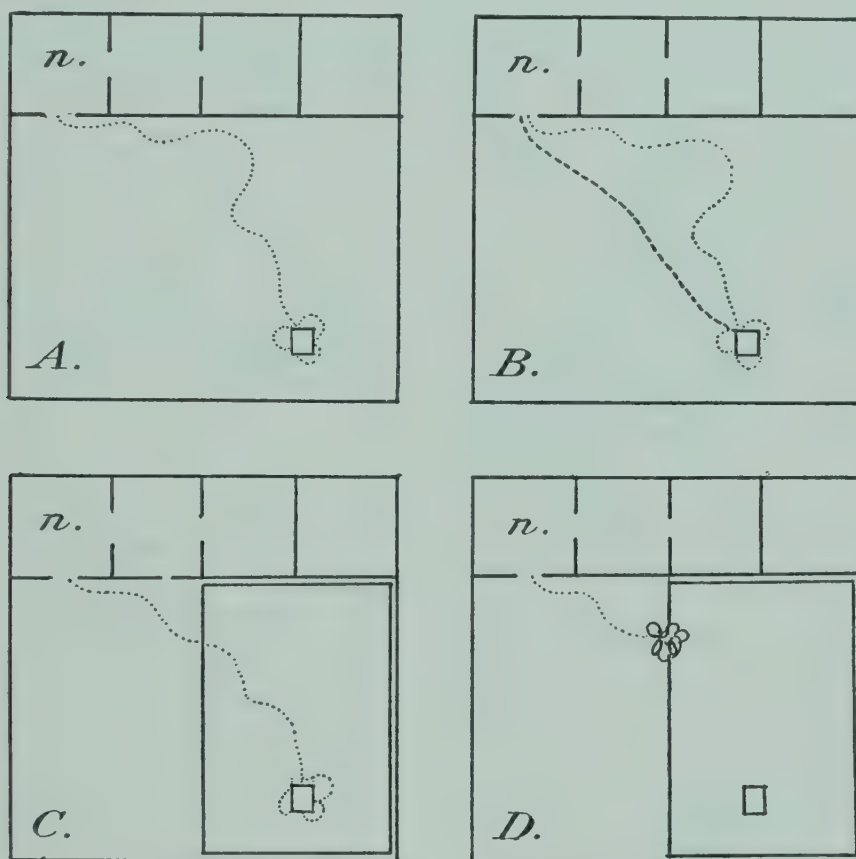


Fig. 106 – GOETSCH's experiment. Diagram A shows how a foraging ant left the nest (n.) and found the food by an erratic path. On a second trip the same ant went more directly to the food, showing that it was guided by visual memory; whereas other ants from the same nest followed the original, twisting path, showing that they were following a scent (Diagram B). At C, a piece of paper covering the ground over half the route did not confuse the first ant, which relied on sight, but the others following the scent (D) stopped at the edge of the paper.

Once an ant has found a promising source of food she makes a number of journeys to it, and other ants are not slow in following suit, so that a well-trodden route soon exists. Along such a path scent and touch are the main guiding senses.

Varnishing the eyes of *Tapinoma*, *Messor*, *Lasius*, and other ants does not much reduce their ability to find the way, but cutting off the antennae destroys this ability completely. The scent left on the ground by the ants

is the principal guide, but not the only one. Touch plays some part. *Formica cinerea* also seems to use sight to some extent, since varnishing the eyes, which normally has little effect, disorientates this particular species completely.

If the trail behind the ants is swept, destroying the scent, *Tapinoma* is completely disconcerted, but *Messor* and *Lasius* are hardly affected, thus indicating that these two genera have additional means of orientating themselves, either visual or tactile.

A striking experiment of Goetsch demonstrates that different senses are made use of by the ant that has found a source of food and the workers



Fig. 107 – *Ammophila* beating down the soil with a pebble held in its mandibles, to conceal the site of its burrow (after PECKHAM).

that come after it: the former is guided by sight, and the latter by scent (Fig. 106). The foraging ant had gone out along a sinuous route, and returned to the nest by a straight line. She returns again to the food along a straight line (by sight), and is not deterred if all trace of scent is suppressed by covering the trail with a sheet of paper. The workers who go back with her, however, follow the original, winding trail, by scent, and are put off if it is covered over.

When they are following a scent, ants are aware not only of its nature, but of its intensity, its distance, and even of the direction in which it has been laid down, so that they can distinguish between the scent of the outward journey and that of the return to the nest. These detailed observations, resulting from a series of experiments, have enabled Forel to present his hypothesis of a 'topochemical sense', to which we have referred earlier.

Language. Insects certainly have a language, in the sense that they can exchange simple ideas with each other. This has been observed mainly in the social insects, notably in the bees, but there is no doubt that phenomena of the same nature, but on a more rudimentary level, may be met with in all groups of insects.

PASSALIDAE, tropical stag-beetles, live in family groups in decaying wood, and call to their larvae by stridulating, the larvae replying in the

same way. Ants are in the habit of tapping with their antennae to attract the attention of other ants when they have discovered a source of food. In bees von Frisch has described and filmed the strange dances of foraging bees, which amount to a true language of the hive. The bee that has found food during its foraging trip returns to the hive and arouses its companions by performing a special dance, differing according to whether the food indicated is pollen, nectar or honey, and moreover varying in length according to the abundance of the material. The workers run towards the dancer, test the scent of an abdominal gland, then spread their wings and fly out of the hive. Experiments show that they then have information about the quality and quantity of the food material, but do not know its exact location. On their return to the hive, these bees, too, perform their dance, so that the number of bees involved grows steadily as long as the food supply lasts.

It is not possible to go into von Frisch's work in detail here, but very beautiful films have been made in which it is demonstrated.

The use of tools. There are very few animals that make use of tools—that is, of objects that they pick up and employ for some particular purpose. The use of tools is generally considered to be a distinguishing mark of the human level, and Bergson has even maintained that the ability to make and use tools defines intelligence. On this definition there exist a few insects that must be credited with intelligence.

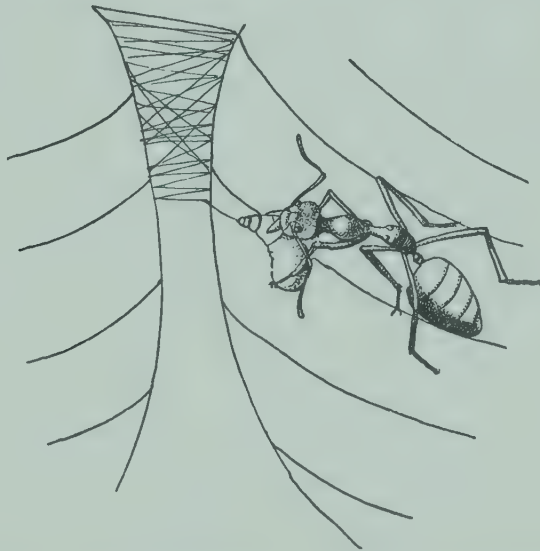


Fig. 108 – The ant *Oecophylla smaragdina* holding one of its larvae in its mandibles, and using it to stitch two leaves together (after BUGNION).

Certainly, the most striking instance is the observation of the Peckhams on American *Ammophila*. These wasps paralyse their prey, and bury it in a hole, closing the opening, and taking the greatest care to destroy all trace of it. To do this, as the Peckhams noted many times, the wasps may use a small pebble to smooth the soil, holding it in their mandibles (Fig. 107), and applying it with short, quick strokes.

Another example is *Oecophylla smaragdina*, an ant found in India

and Africa, which builds nests in the trees by sewing leaves together, edge to edge. To do this, a certain number of workers line up along the edge of one leaf, grip the edge of the next, and pull the two together. Meanwhile one worker seizes in its mandibles one of their own larvae, which is able to secrete silk, and uses it as a shuttle, stitching the two leaves together, while the edges are held in contact by the assistant workers (Fig. 108).

Here the silk-forming larva is used as a simple tool, but the phenomenon is complicated by a division of labour, or rather, by a co-operation of several specialized individuals.

8

Social Life

MANY insects are given to assembling in one place, and even to forming true social groups, and so we may ask if there is not a general tendency towards aggregation among insects. There is, however, a tendency towards solitary behaviour that is equally definite. These two opposing tendencies are not mutually exclusive, and they may exist in succession in the same individual: in the processionary caterpillars, for example, which are essentially gregarious as larvae, but which become solitary as adult butterflies. The two opposing instincts may be present in different forms or castes of the same species, as in the hive where the social instincts of the workers are developed to the highest degree, but the queen is fiercely opposed to the presence of another queen.

The solitary instinct. In a great many insect species not only do the individuals not seek each other's company, but if they should chance to meet another of the same species they fight it, and the victor may eat the other. This has been attributed to competition for food, or for a mate, but this alleged competition may have no real existence.

The instinct for solitude is particularly strongly developed in larvae. A Carabid larvae, for example, cannot tolerate the presence of another of its kind without attacking it, whereas an adult Carabid, though independent in its habits, will rarely go as far as to attack others of the same genus, and may even live in contact with them under the same stone. This anti-social behaviour of larvae is conspicuous in parasites. We never find more than one Codling Moth larva in a maggoty apple or pear, a single larva of *Larinus vittatus* in a thistle-head, a single Plume Moth caterpillar in a grain of wheat. This in spite of the fact that each apple has received in succession the eggs of several female moths, and every thistle-head has been visited by several *Larinus*, while as for the Plume Moth, it lays eggs in batches on the same grain. Two larvae on the same seed or in the same fruit soon meet, and the more vigorous, or the more fortunately placed kills the other and takes its place.

This is not a phenomenon that helps in the evolution of the species; this combative instinct has no practical value. The larva of *Cydia pomonella* has thirty times as much food in the apple as it can possibly eat, and it would be not in the least injured by the presence of two or three others, if it would tolerate them. Moreover, parasitic larvae are sometimes

solitary and sometimes gregarious, without any reason for the difference being obvious. The numerous Hymenoptera and Diptera parasitic on the Cabbage White butterfly fall into two classes. In a single caterpillar of the butterfly there is room for two or three larvae of *Compsilura* or of *Anilastus*, but these larvae will not bear company. By contrast, there may be up to forty *Apanteles* present, in perfect harmony. If a number of *Apanteles* are made to oviposit in one caterpillar, the larvae may be present in such numbers that they die of starvation, but they will not attack each other.

All this shows that the instinct for solitude is not exceptional. It is a primitive instinct, like the social instinct, and the two tendencies are in themselves neither useful nor harmful. We still do not know exactly what brings these rival tendencies into play, but we do know that, as with tropisms, metabolic changes associated with age or sex may cause a reversal of instinct.

ASPECTS OF SOCIAL LIFE

There is not space here to give a full account of the various classifications of social animals, as formerly proposed by Espinas (1878), Girod (1891), and other authors. They are expounded in the excellent little book by Fr. Picard: *Les phénomènes sociaux chez les animaux* (Paris: A. Colin, 1933). Here we can mention only the work of E.-L. Bouvier (1919), who has tried to bring order into the mass of disparate facts relating to the insects.

Bouvier described two types of social life, individualist and communistic, according to whether the individual works entirely for its own ends, within the framework of the society, or whether its labours benefit the others. We may agree with Picard in objecting that, on the one hand, the individualist societies, as conceived by Bouvier, are really family-groups, outside the scope of true social organization; and on the other hand, that the division of labour in a hive or an ants' nest is more apparent than real, and has nothing of communism in it. The common labour of an ants' nest is no more than the sum of the parallel activities of many individuals, responding to the same stimuli, and amounts really to the combined output of a society of individuals. As Forel has written, an ant-heap is neither monarchy nor republic, but anarchy.

Leaving aside, therefore, this arrangement, and others that are equally open to criticism, we follow above all Fr. Picard, who stresses the element of determination in social phenomena. Wheeler (1926), then Rabaud (1929), and above all Grassé (1930) and Picard (1933) hold that the touchstone of the social life is 'inter-attraction', that is a natural propensity or instinct that causes certain animals to be attracted by others of the same species. This arises as a special tropism, a *thigmotropism* (response to a

tactile stimulus) which follows a particular formula. In all other aggregations of individual insects where this tropism is not present, there cannot be any question of a social organization. Such assemblies, brought about by external causes, are merely *crowds* of insects.

Social grouping takes place when there is inter-attraction between individuals, and there is no mystery about it. Whether it is brought about by tactile, visual, olfactory or auditory stimuli, the result is the same, whatever tropism is involved, whether it is the attraction of *Drosophila* by vinegar, of the Pine Scolytid by terebene, or again of nocturnal moths by light. Like every other tropism, mutual attraction is modified by physiological changes in the subject. In many groups of social insects the same individuals pass through a social phase, which is succeeded by a solitary phase.

When, in addition to inter-attraction, there exists also an interdependence, in consequence of which the individuals cannot live without each other, we then have a *biocenosis*, but the term *society* still applies, so long as the group is homogeneous, that is, consists of individuals of the same species. We have to recognize, therefore, three kinds of aggregation in insects: crowds, social groups, and biocenoses.

Crowds. A crowd, or a mass of insects is a chance assembly, usually heterogeneous, including a variety of different species, but sometimes homogeneous, and composed only of members of the same species. The assembly may be only a temporary one, like those of cockroaches or house-crickets, crowding into a warm place, which disperse again if the temperature difference disappears.

Swarms of hatching mayflies, masses of plant-lice on a tender stem, the showers of insects that have often amazed observers—all of these are mere massing, without any internal stimulus to bring the insects together. There is no more inter-attraction, and consequently no social behaviour, about the assemblies that Picard calls 'false animal biocenoses' and which as a rule are vaguely called 'associations'. The fauna of a meadow, living there because they are all dependent on the same vegetational complex, are no more a society than are a group of animals attached to a rock, or a plant community. In all these groups there is some degree of interdependence among the members, but reciprocal attraction between individuals is absent. The assembly comes about solely by the fact that all these individuals of different species find their food in the same place. Their assembly is closely linked with the conditions of the 'biotope' (a setting defined by the existence of certain constant conditions), and constitutes a permanent, heterogeneous aggregation, a *population*.

Certain crowds of insects can give an impression of being a society, as in many Hymenoptera. The communities of *Anthophora* nesting on vertical walls in the sun are like crowded cities. The nests constructed by

the house-martin are like bustling hives. Yet none of these assemblies can be attributed to a social instinct. Each member works for his own profit, and the assembly is brought together only by the choice of a good place for nesting. The names *township* and *colony* could be applied to these homogeneous assemblies, which in fact are no more than crowds.

Social groups. Here the assembly comes about by mutual attraction between the individuals, and we may with truth speak of a social group. Picard distinguished two kinds. One of these, the more simple, has the activities of its members unco-ordinated: in the other kind there is co-ordination of the movements of individuals, in addition to mutual attraction. The activities of a flock of sheep are co-ordinated, and here comes into play, to a great extent, the instinct for imitation. Here we speak of *gregariousness*, which is a social element in behaviour, in contrast to a mere crowd. As Picard says, '*Le phénomène de Panurge est un phénomène gregaire, donc social.*'

Assemblies of this kind are common among insects, and are temporary ones, generally homogeneous. Individuals pass through gregarious phases, during which their behaviour is controlled by mutual attraction, and these alternate with solitary phases, either during the life of the individual, or that of the species. But always, even during the gregarious phase, the individuals maintain their independence, thus differing radically from biocenoses.

Is Picard justified in drawing a distinction between co-ordinated and unco-ordinated societies? We may be permitted to doubt this. Judging from the examples quoted, at least those involving insects, unco-ordinated groups are always assemblies for the purpose of sleeping or of hibernating, of inactivity. In these circumstances it is difficult to be sure that there is no co-ordination in addition to the mutual attraction.

In any case, leaving aside the criterion of co-ordination, is it not better to analyse the assemblies based on mutual attraction into two kinds of social group: *static groups* and *active groups*?

Static groups. Hymenoptera often assemble in their hundreds, and in both sexes, at the approach of winter, to hibernate in trees. *Ammophila* has been seen thus under stones by Fabre, at the summit of Mount Ventoux, in August and September and by Grandi at an altitude of 3,600 feet in the Appenines; while Peyerimhoff has found them under the bark of cedars at 6,000 feet in the Djurdjura Mountains of Algeria. The same occurs in the assemblies of *Pyrrhocoris apterus* (Hemiptera) on tree-trunks and on rocks, or again in the massing of millions of ladybirds that sometimes takes place on mountain-tops on the approach of winter.

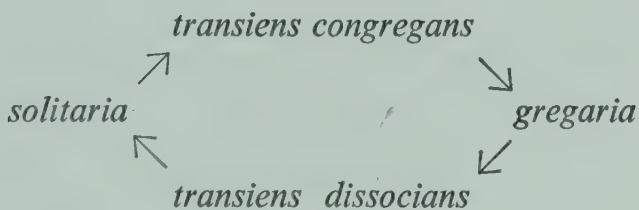
It is easy to explain the mechanism by which these static groups are built up. Allée, in his study of the behaviour of gregarious lower animals, has demonstrated that such a group forms because each individual is

immobilized as soon as it touches another. It is an example of the reflex immobility described above, of tactile origin, which is influenced to a great extent by conditions of temperature, humidity, light, and physiology (the sex, sexual maturity, and nutrition of the individual).

In the same way we can explain why males of *Halictus*, when they come out in the evening, and wander about looking for somewhere to pass the night, 'freeze' into immobility when they come into contact with others of the same species, and so make 'sleeping-groups', composed entirely of males. It is known, too, that ladybirds aggregate in autumn, in vast numbers, on the tops of mountains. A special tropism caused them to climb to the heights, where they come together in various 'trap-areas' (Pictet), where reflex immobility, of thigmotactic origin, spreads outwards at each chance arrival, as if spreading from a centre of crystallization.

Active groups. Recent research on migratory locusts has led to a new understanding of social instinct in insects. It is known that in locusts, as in many Orthoptera, a stock passes through phases that are gregarious and at the same time migratory, and that last for several generations, alternating with solitary phases. Through a series of generations lasting several years, and under environmental influences that are not completely understood, the whole population of one species in the area departs from the normal type, changing colour and pattern in a series of transitions, and at the same time becoming gregarious. Then, in the end, the stock returns to normal, and loses its gregarious habits.

A cycle is thus set up, in which the form *transiens* is established in two or three generations, and then the phase *gregaria* may last from ten to twenty generations before there is a return to the phase *solitaria*.



The remarkable thing is that, as was demonstrated by Uvarov, the onset of the gregarious phase is accompanied by morphological changes so profound that the gregarious and solitary phases of one species may easily be taken for quite distinct species. The same stimulus that determines the social instinct also brings about changes in colour, in the shape of the prothorax (Fig. 109), and in the length of the wings, which are characteristic of the gregarious phase.

In *Locusta migratoria*, for example, the gregarious phase has a low pronotal carena, long wings, and brilliantly coloured hoppers. These individuals in the gregarious phase also have at the same time special

physiological characteristics: their continuous activity, day and night, is associated with an acceleration of metabolic exchanges, an insatiable appetite, a higher body temperature, and even a different percentage of water in the tissues. The reproductive rate is also affected, and is speeded up so that before long individuals are produced in millions.

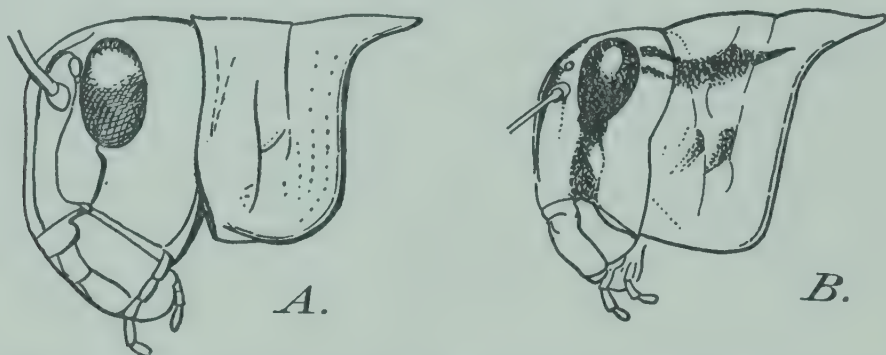


Fig. 109 – Side view of the head and prothorax of *Locusta migratoria* (after VAYSSIÈRE). A, gregarious phase; B, solitary phase.

Observations by Zolotarevsky have shown that the swarming of *Locusta migratoria* in Africa takes place in the delta of the Niger, where the alternating seasonal levels of the water first present the locusts with an immense area in which to proliferate, and then crowd them up into a greatly restricted space. Here the close proximity and mutual stimulation of the insects keeps them constantly moving, and brings about the general acceleration of metabolism, with all its subsidiary phenomena, to which we have already referred.

That this process exists in fact and not merely in theory, has been shown experimentally. It has been possible to bring about the colour changes associated with the gregarious phase in solitary individuals, by placing them in cages that were overcrowded with individuals of a different species of grasshopper (Faure), and also by keeping them isolated, but submitting them to constant excitation by mechanical means (Husain and Mathur).

It follows from this that, at least in ACRIDIDAE, inter-attraction is not the primary cause of gregarious behaviour. These assemblies are originally mere crowds, brought about by some external cause, such as the fluctuations in area of the delta of the Niger. A crowd of this sort among ACRIDIDAE, however, is different from that of many insects, because the assembled individuals are endowed with a special thigmotactism, which converts this mechanical stimulus into an acceleration of metabolism, and into a new physiological state which leads on to morphological changes, to the appearance of the social instinct (inter-attraction), and at the same time to the migratory instinct.

The gregarious state brought about in this way, and maintained moreover by the accelerated rate of reproduction, is manifest as a co-ordination of the movements of individuals, as a result of which contact is renewed and kept in being. This co-ordination sometimes arises from inter-attraction itself, and sometimes also from an instinct for imitation which is developed quite independently.

Migration

The ACRIDIDAE, therefore, throw light on the correlation that exists between the social state and the migratory instinct, and enable a link to be shown between their periodical gregariousness and the large-scale migrations that have been seen many times in different groups of insects. Migrants of this sort do not show morphological changes, but their

Fig. 110 – *Danaus archippus*, from North America.



gregariousness may well be determined in something of the same way as that of the locusts.

The Danaid butterfly *Danaus archippus* (Fig. 110) is distributed throughout the two Americas, and its caterpillar lives on *Asclepias curassavica*. The butterflies breed in South America, and every year make a migration from South to North and back again, like the migrations of birds. From time to time they produce a vast migration, involving millions of individuals at the same time, and covering tremendous distances, even across the ocean. In this way the species has crossed the Pacific and reached both the Hawaiian Islands and Australia. It has also crossed the Atlantic and become established in the Canaries, where its larval feeding-habits have been modified to suit *Gossypium arboreum* and *Euphorbia mauretanica*, plants belonging to the African flora. In this way colonies of non-migrating butterflies have been established, in distant places, by migrations of the gregarious ones.

In Europe, immense numbers of migrating Painted Lady (*Vanessa*

cardui), or Cabbage White (*Pieris brassicae*) butterflies have been reported, the former species having become almost cosmopolitan. Pictet, who watched a big migration of *Pieris* in Switzerland, records that migrant individuals do not fly in the same manner as those that are not on migration. They have a higher speed, and fly straight ahead, without stopping to feed. It seems as if the social grouping has its origin in a changed physiological state, as in the locusts.

Mass migrations have also often been seen in Odonata, and in Coleoptera, such as *Ophonus*, *Hoplia* and *Callicnemis*. They can also be seen in the larvae of some insects, such as the 'Army Worms', larvae of the fly *Sciara militaris*, which moves in columns on a front of several feet and a length of several yards. The larvae are pressed one against another, and joined by their sticky secretion. At first they form small bands, which pick up neighbouring bands on the way, and so build up great armies, like a living and moving tablecloth, formed from maggots stuck together.

The caterpillars of many Lepidoptera live in communities in silken nests which they weave jointly. These are social groups that are almost on the boundary of true societies. There still does not appear to be a complete interdependence among the individual insects, but they are already linked together by subordination to a common task. The best-known example is that of the Processionary Caterpillars, that of the Pine (*Thaumtopaea pityocampa*) and that of the Oak (*Th. processionnea*). When they are on the move, the thigmotactism of the caterpillars is evident from the formation of chains, in which the head of each individual is held in contact with a tuft of stiff hairs at the tip of the abdomen of the preceding one.

Like the other social assemblies, that of the Processionaries is temporary, and ends with the end of the larval period. It is determined solely by inter-attraction. There is no mutual understanding, no interdependence, in the occupation of the caterpillars, while they move steadily along, ignoring their neighbours on each side.

Biocenoses, or Societies. Like the social groups we have just discussed, biocenoses rest on an inter-attraction, but they differ fundamentally in that the interdependence of the individuals is the predominant factor. The members of a biocenosis cannot live alone.

All kinds of associations of individuals of different species can be found, in all kinds of setting, each forming a perfectly balanced biocenosis. There is an attraction between individuals, which is not always mutual, and which may be replaced by simple tolerance. Such *heterogeneous biocenoses* are very common among insects, sometimes associating only two species, sometimes a great many, each more or less dependent on the others.

In the most simple examples, one species makes use of a setting created by the other, like the beetles of the family IPIDAE, genus *Dendroctonus*, which make their way beneath bark by using the air-channels cut by other IPIDAE. Making use of the quarters of another insect in this way may lead on to making use of its faeces, exuviae, food-stores, or even of the host insect itself, and so by gradual stages to kleptoparasitism and to predation.

In the cones of the Aleppan Pine of the Mediterranean region a biocenosis exists between a Tineid, a mite, and a Staphylinid beetle, which has been described by Picard. The caterpillar of the moth (*Dioryctria mendacella*) excavates a gallery, in which a coprophagous mite (*Pronematus bonatii*) lives and is preyed upon by a Staphylinid (*Placusa nitida*). Triple associations of this kind are common, bringing a scavenging mite and a predatory Staphylinid into the gallery of a boring insect. The biocenosis that has developed in the galleris of the Scolytid beetle of the Fig (*Hypoborus ficus*) is much more involved, and brings together a great number of interdependent species.

A *homogeneous biocenosis* is one composed of individuals of the same species, in close dependence upon each other. It is convenient to use the term 'society' for such an association, within which the members are so narrowly dependent on each other that they are no longer able to exist outside the society. Biocenoses of this kind are most often family groups, all the members being descendants of one female, or of a small number of females.

The ones always quoted are bees, wasps, ants and termites, but there are others less highly perfected, which it would be interesting to know more about—for example, the BRACHINAE, which Picard considers as simple, unco-ordinated social groups. These CARABIDAE, well known as Bombardier Beetles, live in societies under stones, and are often very numerous. These associations generally contain only one species, but are sometimes found to include several nearly related species: for example, *Brachinus crepitans*, *explorens* and *sclopeta*, with which a Carabid of a totally different group, though of similar size and colour, *Platynus dorsalis*, may mingle.

Although the adults are so common, the larvae of the greater number of *Brachinus* are unknown. No doubt if their life-history could be discovered it would throw light on their societies, which form year after year under the same stones, and seem to have the character of biocenoses, although rudimentary ones. The fact that homogeneous biocenoses are most often family groups does not imply that they had a family link originally. Both sexes of *Copris* co-operate in feeding their young, and earwigs may be seen surrounded by their offspring (Fig. 87), but these are not the beginnings of biocenoses. Nor are the longevity and fecundity

of the females responsible for such biocenoses, but most often are a consequence of the social organization.

In homogeneous biocenoses inter-attraction takes a special form, involving the exchange of food among individuals (the *trophallaxis* of Wheeler), and the feeding of larvae. These are often complex phenomena, which have no equivalent among solitary insects, with very rare exceptions (*Necrophorus*).

At one stage of evolution of homogeneous biocenoses the specialization of the individual insects becomes evident by the formation of *castes*. A



Fig. 111 – Social wasp of the genus *Belonogaster* (after PICARD).

special kind of polymorphism arises, generally among the females, of which a few remain fertile, but the rest become sterile, and form castes of workers and soldiers.

Finally, Picard defines a category that he calls *complex biocenoses*. In an ant-hill or a termitarium all kinds of commensals and parasites are in occupation, living in interdependence with their hosts. As a further step, entire communities may join forces in the same nest, bringing with them their respective followings of commensals and parasites, and so reaching a maximum degree of complexity.

THE SOCIAL INSECTS

It would not be possible to describe in this volume all the tremendous variety of insect societies that are known to exist, so we must be content with a detailed description of a few of them, trying particularly to understand how they may have evolved.

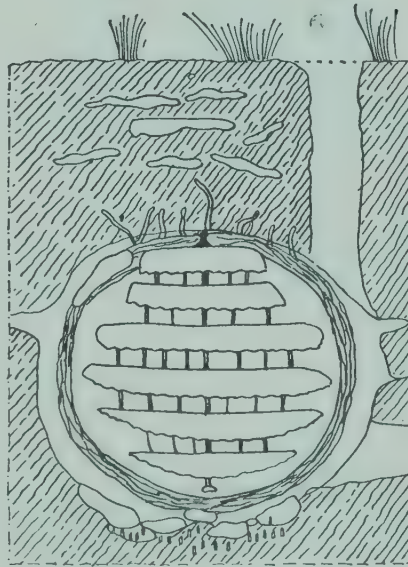
Wasps. Among wasps there can be seen all stages from a solitary to a social state. Under this heading the tropical species are particularly interesting, and the work of Roubaud on the wasps of tropical Africa has opened up a field of study that is still almost unexplored, and which presents entomologists with ample scope for research.

Many societies among wasps are polygynous, that is come about by the collaboration of several females. In Africa, the colonies of *Belonogaster junceus* are built up exclusively by fecund females joining forces with each other. In the colonies of *Icaria* the females are more numerous than the workers, whereas in *Polybia* there is only about one fertile female to every six others.

In *Belonogaster* (Fig. 111) the first eggs to be laid hatch into females which stay close to their mother, and give her help until the arrival of the males, which hatch later. As soon as they have been fertilized by their brothers, these females disperse to found new colonies.

The wasps show how castes may have arisen. If the female lays too many eggs she can no longer give them enough to eat, and the under-fed larvae suffer a *nutritional castration*. Their gonads fail to reach maturity, and are atrophied; these insects become sterile workers, helping their mother in the nest. The larvae hatching from later batches of eggs are better nourished, and once again give fully-sexed individuals, which swarm. The various species show all stages of an evolution which comes near to creating a true worker caste of morphologically distinct individuals. The polygynous societies of wasps thus resemble the bees in being perennial, and in swarming.

Fig. 112 – Underground nest of *Vespa germanica* (after JANET).



It has not been proved that the monogynous societies of wasps have arisen directly from the polygynous ones. The monogynous societies are annual: all the workers die each autumn, and only the fertilized female hibernates, to found a new colony in the spring.

In temperate countries the monogynous colonies of *Vespa* are highly evolved. *Vespa germanica* builds nests of paper, from masticated wood, arranged in horizontal combs, surrounded by an envelope with a hole underneath (Fig. 112). The cells are on the lower surface of each comb,

and in these the larvae are fed every day, instead of being provided with a store of food.

The nests of *Vespa* harbour both commensals and parasites: Diptera (*Volucella*), Coleoptera (RHIPHOPHORIDAE), and Strepsiptera (*Xenos*). The Strepsiptera are endoparasites and bring about in female wasps the malformations that are known as 'stylopization'. A stylopized wasp is

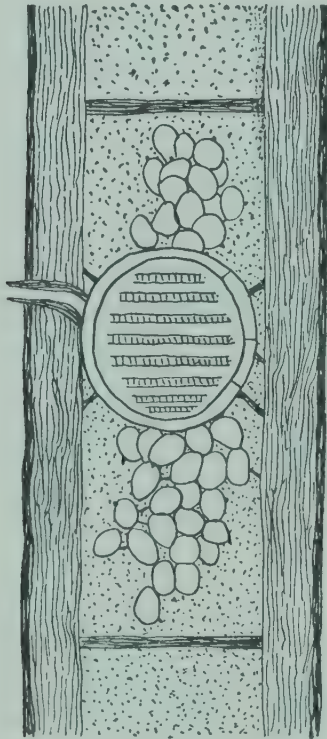


Fig. 113 – Nest of *Melipone* in a hollow tree (after JHERING). The honey-stores are outside the nest proper.

always a female, and takes on characters that properly belong to the male sex (*parasitic castration*). The caterpillar of a moth (*Melissoblastes anellus*), protected by a tube of silk, devours the substance of the nest, and plays a similar part in wasps' nests to that of the Wax Moth, *Galleria mellonella*, which attacks the wax of bee-hives. A big Staphylinid, *Velleius dilatatus*, lives as a commensal in the nest of the Hornet, and infests this with mites (*Tyroglyphus longior*) by bringing them in on its body.

Bumble-bees (humble-bees). Bumble-bees are nectar-feeders, unlike the carnivorous wasps, but their societies are similar. In the tropics they are perennial and polygynous, and in temperate countries monogynous and annual, just like the wasps.

The nests of bumble-bees are subterranean, made out of a mixture of earth, resin and wax. Some cells are used for rearing larvae, and other, different ones are storehouses for honey. The larvae that are to develop into queens do not get any special food, but simply a greater quantity than larvae destined to become workers. The males are produced by parthenogenesis, and are the last to appear. In temperate countries the

whole colony perishes in winter, except for the fertilized females, which hibernate.

In Europe the nests of bumble-bees have an interesting commensal in *Leptinus testaceus*, a little, blind beetle, which is sometimes very abundant and which seems to be spread from one nest to another in the fur of small rodents which have a taste for honey. Other beetles (*Antherophagus*), live on flowers, and cling to the legs of bumble-bees so that they are carried back to the nest, where they scavenge among the debris.

Meliponinae. These are wild bees of South America, whose social life is quite different from that of the hive-bee. The societies are polygynous, and the worker caste is morphologically quite distinct.

MELIPONINAE nest in hollow trees (Fig. 113). The nests are built up from horizontal combs, like those of wasps, and are surrounded by an envelope, outside which are placed external stores of honey, pollen, propolis, and a special resin, the cerumen. The cells are provisioned in advance, and are then closed after eggs have been laid in them. It is still not known whether the queen-larvae receive any special food. The males arise parthenogenetically, from unfertilized eggs, like the males of bumble-bees and hive-bees, and they labour in the nest like the workers.

Unlike the hive-bee, it is the young queens that swarm, and not the old ones, which become so fat that they cannot even fly.

A special group of Liodid beetles, the genus *Scotocryptus*, lives as a commensal in the nests of MELIPONINAE.

Hive-bees. The nest of the hive-bee is the most highly evolved of the homogeneous biocenoses among bees, and is a monogynous society.

In the hive the combs are vertical, and have cells on both sides, built from wax. The same cells serve equally well for rearing larvae or for storing honey. The larvae are fed day by day, and not provisioned once and for all, like the larvae of MELIPONINAE. Moreover, the cells are left open, and are closed only at the time of pupation. One or two specially big ones (royal cells) contain larvae that are given a special food ('royal jelly'), which is concocted by the workers. These larvae turn into queens. The larvae of workers, and those of males, receive only a mixture of honey and pollen, but a worker-larva can be turned into a queen bee if it is transferred to a royal cell when it is a few days old, and fed on royal jelly.

The old queen tries to kill the daughter-queens as soon as they are adult, and sometimes even sooner, but the workers protect them. When the workers come to the rescue the old queen abdicates, and leads a swarm away from the nest. It is said that about half of the population of the hive joins the swarm, which may involve from half an ounce to more than two pounds of bees.

The queen can control the sex of the eggs she lays, by closing her

spermatheca at the moment of oviposition. This results in the laying of unfertilized eggs, which are placed in bigger cells than the workers, and give rise to males (*drones*).

The hive does not have as many commensals as the ant-heap or the termitarium, by a long way. The most common are the two Wax Moths, *Galleria mellonella* and *Achroia grisea*, and a blind and wingless fly, *Braula caeca* which parasitizes the queen, attaching itself to her thorax and robbing her of some of her strength.

Ants. Social life among the ants is most highly evolved, and immensely varied, with a great range of nesting habits. The greater number of nests are subterranean, a labyrinthine network of galleries, with one or more entries, with breeding chambers, and storehouses for provisions. A cone of turf and twigs, sometimes a high one (*Formica*), often covers the entrance.

Many ants do not live underground. Some (*Leptothorax*) make a nest in rotting wood, others in green wood, which they tunnel (*Camponotus*). African *Cremastogaster* produce galls on certain acacias, and then excavate them, to make themselves aerial cities. Some ants build their nests of masonry; others (*Cremastogaster*, *Azteca*) build paper nests, often of great volume, high up in trees, Pl. 2, IX (D), and we have seen already how *Oecophylla* makes use of the silk-glands of its own larvae to stitch together the leaves of trees to make a cover for the nest.

The winged sexual forms come out in great numbers at certain times of year, and mate during a nuptial flight, then the females found their colonies, either from one female alone or from several in conjunction. In some species the workers are minute in size, and cling either to the winged females (*Carebara*), or to both sexes (*Solenopsis*), so that they are carried up into the air on the nuptial flight. They are then at hand to help the females to found their colonies. The fertilized females first dig out a shelter for themselves, then lay eggs in it, which they nurse all through the winter, licking them constantly, but not themselves taking any food. When the young workers hatch in the spring they take over the feeding of the queens.

Ants are often polymorphic, with many castes, but the way in which the castes are determined are not yet completely understood. It seems, however, that they arise by an interplay of two factors, one cytoplasmic and so laid down in the egg, the other depending on the quality and quantity of food.

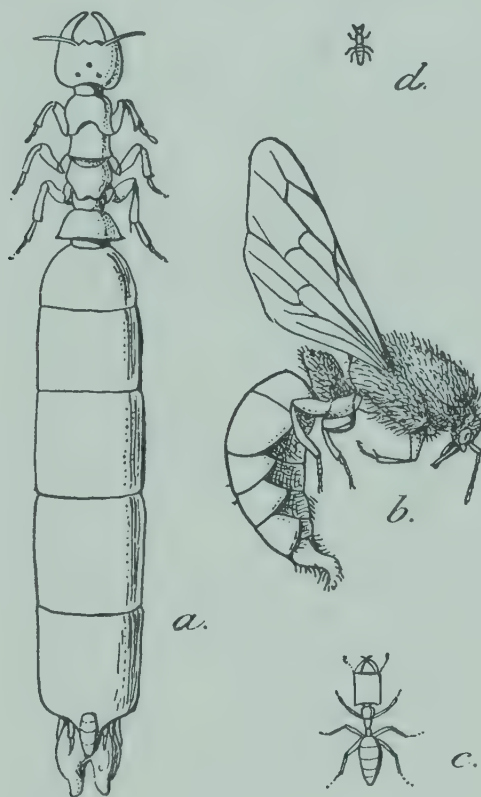
Worker ants are females whose gonads have not completed their development. They may differ greatly in size within one species (*Pheidole*). There may also exist, as in the Amazon Ants (*Polyergus*), or the Ponerinae, females that are intermediate between queens and workers. These are called 'ergatoids', since they are like workers, but with the ovaries fully

developed. Some *Ponera* have polymorphic males, some with normal eyes and wings, others (ergatomorphic males) apterous and with reduced eyes. In certain wingless males of *Anergates* we have even a further stage of degeneration, where the males look like pupae, and never leave the nest.

Driver Ants

The Driver Ants (DORYLIDAE) are a very primitive family, with unusual habits. They are African ants, of carnivorous diet, and live in deep subterranean nests, most often at the foot of trees. Here is to be

Fig. 114 – Polymorphism of the castes of the Driver Ants, Dorylidae (after HANDLIRSCH). a, the female; b, the male; c, a big-headed worker or soldier; d, a small worker. The four insects are drawn to the same scale.



found the queen, which is enormous like the queen termite, and is surrounded by a great number of workers (Fig. 114). The males are big, and winged, looking like big, reddish wasps, and are well known because they come regularly to lights at night. The identification of the males is difficult, however, because it is only rarely that they can be correctly associated with the queens and workers of their species.

The workers are totally blind, small, and provided with a sting, and are of two types. They are the ants that march ceaselessly in immense columns, and the two types of worker have different functions. Those with small heads march in several columns, some carrying their pupae, some various commensals from the nest. The other workers have big heads, and strong mandibles, and march on the flanks of the column

their heads turned outwards, and their mandibles at the ready, to deal with any foe. In some species these 'soldiers' build themselves into a tunnel of living ants, through which the files of small-headed workers march steadily. As the tail of the column passes them, the soldiers at the rear go forward to the head and take up station again there. Every obstacle that the ants encounter is overrun; every living being is attacked by uncountable numbers, stung to death, and devoured.

Woe to the traveller who is taken by surprise at night in his tent by the arrival of a column of *Anomma*! True, he is not killed and eaten, but he is forced to flee, harassed by the bites and stings of the ants. It is said in Africa that it is less dangerous to meet a lion than a column of Driver Ants.

What is the purpose of these migrations, and how does it connect up with the subterranean nests where the sexual forms live? Almost nothing is known. The nests and the female ants have only recently become known, through the discoveries of van Someren in Kenya, and the habits of Driver Ants are still a vast field for observation and study. It is known that they have particular commensals, some of which march in the middle of the column, and others get themselves transported.

Harvesting Ants

These ants belong to a group that is more highly evolved than the DORYLIDAE, namely to the genus *Messor*, which is common in the Mediterranean Region and in the Sahara. Their subterranean nests are extensive, and go down several metres into the ground, and are surmounted by a dome that may be fifty centimetres high. Following well-worn tracks the ants forage for seeds, which they store in underground granaries. After a rainy period the ants put their seeds out to dry in the sun, but they do not sow or cultivate them, as used to be thought by those who had seen the seeds germinate as they lay near the entrance to the nest. The big workers masticate the seeds into a paste, which others dry, and then feed to the larvae.

Mushroom Gardens

Atta, an American genus, go out in procession to look for leaves, which they carry back to the nest, holding them vertically in their mandibles. Pl. 2, VIII (A). This earns them the common name of 'Parasol Ants'. When they get back they sow spores of a fungus (*Rhizites gongylophora*) on the fragments of leaf, and so cultivate 'mushroom gardens'.

These are constructed in chambers which extend under the ground, and are often more than a yard long. They have several openings to the exterior, and the ants can open or close these to regulate the ventilation. The ants manage to maintain a pure culture of the fungus, without any

contamination by other spores, but how they do this is not known. At certain times the females migrate to found new nests, taking with them hyphae of the fungus, carried in the mouth. On first planting the fungi in the new nest the ants manure it with their own excrement, or with some of their eggs, which they crush. The female which founds a new nest does not feed herself, but feeds her larvae on crushed eggs. When these larvae have become adult they continue to feed the younger larvae in the same way. It is only when the workers have been able to collect enough leaves to make a proper mushroom garden that they begin to feed the larvae on hyphae of the fungus.

Attaphila, a genus of small cockroaches that lives in the mushroom gardens of *Atta*, licks the ants, but does not steal their fungus. A big parasitic beetle (*Physea*) also lives in the nests of *Atta*, its larvae living and pupating in holes excavated round the edges of the mushroom gardens.

Honey Ants

Ants of the genus *Myrmecocystus* turn some of their workers into living receptacles for honey, and these are known as repletes. Pl. 2, VIII (D). MacCook and Wheeler in North America have observed these ants, and seen them lick the sugary excretions of aphids, or the honey-like matter that exudes from plants on cold nights, or which can be extracted from certain galls. This sugary material is then deposited into the crops of the big workers, which swell visibly, and may reach, or even exceed, the size of a pea.

These repletes cling to the ceiling of a special underground chamber, which is dug out in hard, dry soil, and provided with good ventilation. Here they are visited from time to time by normal workers, which come either to add to their store, or to persuade them to disgorge some of their honey-dew by coaxing them with strokes of the antennae.

Certain *Camponotus* of the Mediterranean Region have somewhat similar habits, but less fully developed. Other honey-ants are *Melephorus* of Australia and the South African *Plagiolepis jouberti*, but in all these the repletes are still able to move about.

Ant-stables

A number of other ants beside *Myrmecocystus* exploit the sugary excretions of Aphids. Some, like *Leptothorax*, content themselves with licking the Aphids if they happen to meet them accidentally, but many ants actively search for the Aphids, or even keep them and rear them in 'stables'. Pl. 2, VIII (B, C). *Lasius* carries its Aphids about on twigs, and tends them like domestic animals, and some species install the Aphids in stables round about roots, upon which the Aphids can feed. The ants allow the sexual phases of the Aphids to come out and mate, and know

PLATE 2 – VIII. ANTS

- A. Fungus-rearing ants. Two workers of *Atta* ('parasol ants') bringing back pieces of leaf which are accumulated in the nest to form the fungus-garden (South America).
- B. Ant-stables. Plant-lice (*Trama radialis*) on the roots of *Artemisia*, and guarded by *Lasius umbratus* (after FOREL).
- C. An underground stable in which *Lasius flavus* are grooming their domesticated Aphids.
- D. Honey-ants. *Myrmecocystus* in North America converts certain workers (nurses) into honey-pots, which they hang from the roof of their underground chamber, and whose exudations they lick. Below, a nurse-ant in side view (after FOREL).
- E. A Thysanuran living with ants. *Atelura formicaria* snapping up droplets of food disgorged by their hosts, **Formicina**.
- F. An aerial garden of *Azteca*, with epiphytes growing out of it, in the Brazilian forest (after ULE).

PLATE 2-VIII. ANTS



where to find the eggs that the females lay. The eggs or the young Aphids are collected and taken back to the stable. Thus, certain species of Aphids are linked with *Lasius* in a very close symbiosis.

In Ceylon, *Iridomyrmex* rears Psyllids in the same way; in the United States, *Formica integra* exploits hoppers of the family MEMBRACIDAE; and in Algeria, a *Tapinoma* maintains stables of FULGORIDAE under the bark of *Tamaris*.

Moreover, the Homoptera are not the only groups of insects to be domesticated by ants. Caterpillars of Lepidoptera are equally used, especially those of *Lycaena*, the group of well-known small blue butterflies. Certain caterpillars of this group live dispersed among plants (Leguminosae), and are licked by ants. Those of other species are reared in the ant-heap, and there they pupate. The emergent butterfly escapes from the ant-heap, protected from the fierce attacks of the ants by a temporary carapace of sticky hairs.

Slave-making Ants

Here we have the extreme development of a complex biocenosis. Certain species from time to time make raids on the nests of other species, and carry away pupae, which they rear in their own nest. The captive ants which emerge meekly wait upon their captors.

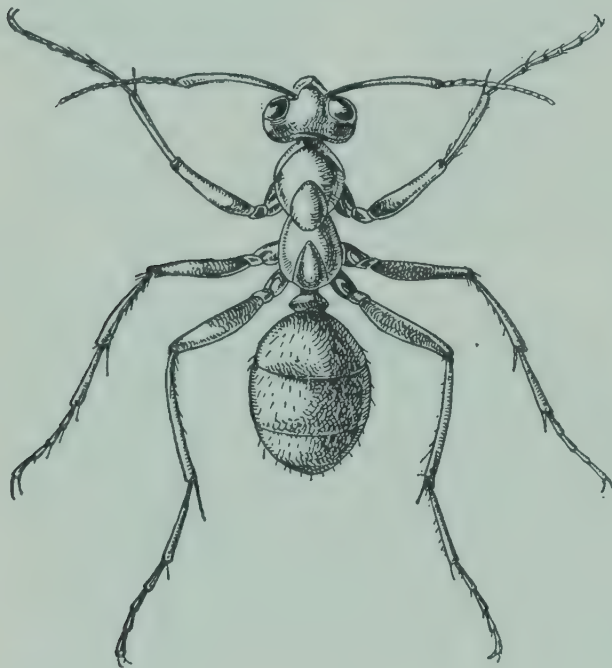
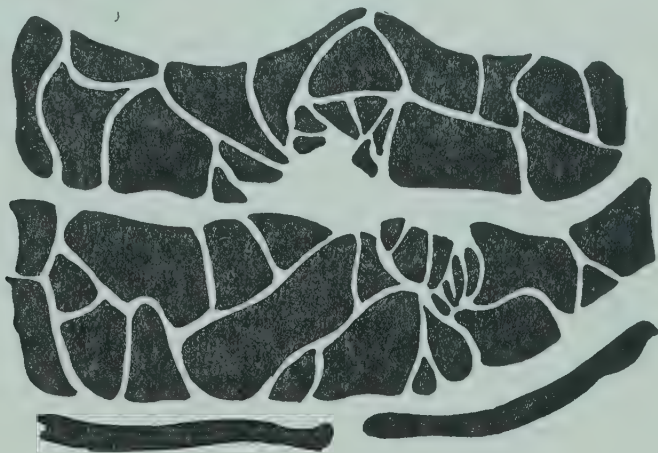


Fig. 115 – A worker of *Formica fusca* (after PICARD).

The sequence of events during the founding of a colony by *Formica sanguinea* is well known. The queen *F. sanguinea* penetrates into the nest of a colony of *Formica fusca* (Fig. 115) and possesses herself of several pupae, repelling the attacks of workers which try to get them back from

her. She can do this with little difficulty, because *fusca* is by nature much more timid and peaceful than the aggressive *sanguinea*. In due course the pupae hatch, and the adult workers emerging from them wait upon the queen *sanguinea* and feed her and her progeny. Bit by bit the growing colony of *sanguinea* get themselves adopted by the colony of *fusca*, and even induce the *fusca* workers to kill their own queen.

Fig. 116 – A nest of *Solenopsis fugax* (narrow galleries) inside one of *Formica fusca* (broad galleries) (after WASMANN).



Later on, the colony of *fusca*, deprived of their queen, begin to decline, and to reinforce them the *sanguinea* workers that have just emerged make raids upon other nests of *fusca* in the neighbourhood. These raids come to an end after a time, when the *sanguinea* workers have become numerous enough to support themselves as a pure colony.

Formica sanguinea can thus eventually dispense with slaves; *Polyergus* is never able to do this because the workers have reduced mandibles and cannot feed themselves. They can never obtain food except by being fed by slaves, and their only occupation is slave-raiding—once more against *Formica fusca*. Other species have pushed their evolution a stage farther; *Strongylognathus* uses the slaves themselves as a raiding-party.

Slavery in ants is thus a special form of paratism. We see another form of this when whole colonies of one species live in the nest of another species, and are dependent upon them, as in *Solenopsis fugax*. This is a diminutive ant, which makes the galleries of its nest interlace with those of *Formica rufa*, and so is able to steal a part of its food from the *rufa* nest without much danger to itself (Fig. 116). This is a sort of collective kleptoparasitism. In America, the small ant *Trachymyrmex* sets up its own mushroom garden within the garden of *Atta*, from which it steals its spores.

Myrmecophiles, or Commensals of Ants

Nearly 2,000 species of Invertebrates are known to live in a state of dependence on ants. The relations between these *myrmecophiles* and their hosts are most varied, and have been grouped into several categories.

The simple commensals, or *synoeketes* (Wasmann) are merely tolerated in the ant-heap, and do not cause much trouble to their hosts. They usually feed on debris, or excreta, but sometimes lick the ants and may even steal food from them. A tremendous number of species fall into this category, and it is impossible to list them. They include a small whitish wood-louse, *Platyarthrus hoffmannseggi*, which is abundant in certain ant-colonies under stones. The Thysanuran *Atelura formicaria* comes to lap up droplets of food when the host ant, *Formicina*, regurgitates them. Pl. 2, VIII (E). A little, blind cricket, *Myrmecophila acervorum*, which is parthenogenetic, licks up the exudations from the bodies of the ants that shelter it.

A more highly evolved group are the *symphiles*, which live on good terms with their hosts, are groomed and fed by them, and give them services in return. A distinguishing mark of symphiles is the possession of *trichomes*, masses of secretory hairs which the ants lick unceasingly. The greater number of symphiles are beetles, cherished by the ants, and carried with them wherever the nest is moved, but nevertheless terrible enemies of the colony because of the great damage they do to it.

Paussus and *Claviger* are common in ant-heaps, especially in hot countries, and Staphylinids of the genera *Atemeles* and *Lomechusa* come into the category of symphiles. *Lomechusa strumosa*, cherished by *Formica sanguinea*, devours the larvae and eggs of its hosts, which, growing fewer and fewer, exhaust themselves to feed their lodger. Moreover, it seems as if the secretion of the trichomes has an effect on the ants similar to that of alcohol on humans, so that a colony of ants that is bewitched by *Lomechusa* takes the road to degradation and extinction.

The category of *synechthrans* comprises all the myrmecophiles that impose themselves forcibly upon the ant colony. This is the case, for example, in *Myrmedonia*, tiny Staphylinids that the ants detest, but which keep them at bay by using a corrosive liquid. Although perpetually harried, the beetles eventually manage to eat some of the brood, and sometimes even some of the workers.

Some synechthrans are protected by a carapace, by being very small, or by having such a shape that they can cling closely to the substratum, and not project enough for the ants to seize them with their mandibles.

Finally, there are true *parasites*, like the Nematode worms of the genus *Mermis*, which are endoparasitic in the larvae. These feed insatiably, and produce giant pupae and deformed adult insects.

Termites. The biology of termites is not as varied as that of ants, but has been much less studied because termites are more difficult to observe. Because of the great economic importance of these insects—some of them cause enormous damage by destroying wood, while other species are beneficial—it would be a good thing if there were more laboratories set up in tropical countries to make detailed studies of the various species.

Something has been done in this direction by *l'Office de la Recherche Scientifique Coloniale* in France, and by the Commonwealth Institute of Entomology in London.

CASTES. In termites the formation of polymorphic castes has progressed even further than it has in ants. Within a termite colony there is a royal couple—sometimes several—and different types of neuters, workers and soldiers, large, middle-sized and small. Here the workers may be either males or females with aborted gonads, and not females only as in ants.

The sexual individuals have wings at the time of swarming, and generally are much bigger than the neuters, with compound eyes that are very convex. In the termite colony the queen becomes enormously distended with eggs, and the king remains beside her, mating with her several times during her lifetime, which may be as long as ten years in some species. In the more advanced termites the queens may lay nearly fifteen million eggs in the course of a long life. The immature termites are active, but never leave the termitarium.

The workers look after the young, and are always wingless. Those of the primitive species have eyes (*Hodotermes*) and may come out into daylight, but those of the more advanced groups are blind, and rarely emerge from the nest. There are several categories of workers, distinguished by their size.

The soldiers are generally bigger than the workers, but are also wingless and blind; they always have a big head and this is especially so in the larger species. In many species the soldiers are armed with big, long mandibles, variable in size, which are generally pincer-like, but sometimes serve as jumping organs (*Mirotermes*). The *nasute soldiers* of *Eutermes* (Fig. 117) have the mandibles atrophied, but are equipped with a frontal horn, which acts as a squirt to project a sticky liquid over the enemy. Under certain stimuli the soldiers, and the workers as well, can make a collective noise by beating their heads against the ground, but it has not been shown yet whether this method of sound-production is in fact used as a means of communication.

In certain species we find, also, males and females that are not completely developed, and which are called 'neotenic forms'. These may be numerous in one nest, and it seems probable that they are a kind of reserve, from which the king or queen could be replaced in case of need.

FOUNDATION OF A COLONY. At certain seasons of the year the winged sexual forms leave the termitarium in a body, and take part in a swarming of 'white ants'. The moment they come out they are attacked by a multitude of enemies, mammals, birds, reptiles, but a few of the termites survive, and settle on the ground, or on vegetation. The winged forms are still not sexually mature at the time of swarming, but nevertheless they pair off, and shed their wings. Each pair then digs itself a nuptial chamber,

in which they develop to maturity before pairing and oviposition. Each nuptial chamber becomes the nucleus of a new termite colony.

NUTRITION. Termites are polyphagous. The workers live mainly on wood, but also on vegetable matter, either green or dry, and on animal products, hides and skins, or even ivory. The lower termites (*PROTERMITIDAE* and *MESOTERMITIDAE*) have intestinal flagellates (Fig. 63) and bacteria which can digest wood, and which are indispensable to the life of the termite. This is not so in the higher termites (*METATERMITIDAE*), which have no wood-feeding Protozoa. It is still not known how these termites can digest cellulose.

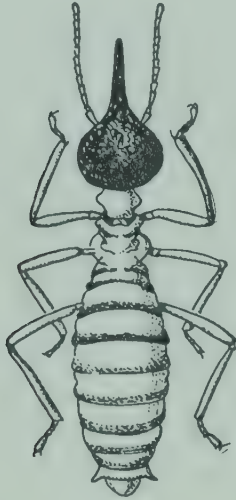


Fig. 117 - A nasute soldier of *Eutermes* (*Metatermitidae*) (after IMMS). The frontal horn is a syringe, from which a sticky liquid can be squirted at an enemy.

The workers and the soldiers are the only members of a termite colony that can support themselves by foraging outside the nest. In addition, at least among *PROTERMITIDAE*, they can obtain food from each other by sucking either at the mouth or at the anus. The sexual forms, the immature stages, and those soldiers of the higher termites that have the mandibles too highly specialized for them to be suitable for feeding, all have to rely upon the workers to feed them. The workers give them either stomodeal food, which they regurgitate, or proctodeal food, which they pass through the anus. Proctodeal food goes mainly to the workers; stomodeal food, consisting of pre-digested cellulose mixed with saliva, is primarily the food for immature stages and for the sexual forms, and no doubt varies in content accordingly.

The workers that look after the royal couple have certain perquisites from the office. They make use of liquids excreted by the queen, and lick up fluids exuded in response to caresses, or even obtained by piercing her distended abdomen. We shall see later on that the fungus gardens play only a very minor part in the nutrition of *METATERMITIDAE*.

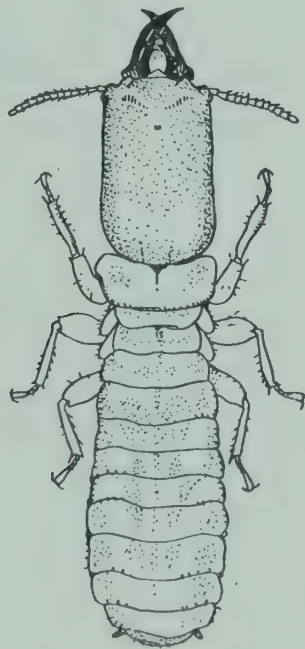
TYPES OF TERMITARIUM. The varied kinds of termitarium can be arranged in some sort of classification. Holmgren puts them into two

categories: *diffused nests*, with an irregular system of galleries and chambers; and *concentrated nests* with well-defined outer limits, and with several rings of chambers round a central nucleus. Pl. 2, IX (A–C). Concentrated nests are built either from soil, or from a cement made from soil and wood, or again from a paper made from pure wood. Some of them are subterranean; others are built above ground-level and may be structures of great height (up to more than 10 metres in *Bellicositermes jeanneli* in the area round Lake Rudolph: Pl. 2, IX (B); finally, others are built in trees, from cement or paper. Concentrated nests are built by the higher termites, the METATERMITIDAE.

PROTERMITIDAE. These are the most primitive termites, whose nests are not concentrated, and for the most part are in dead wood. *Calotermes flavicollis* of Central France belongs to this group. Their castes are weakly developed so that besides the royal couple there are only soldiers, and no workers (Fig. 118). The immature termites take the place of workers, and labour in the nest.

Swarming time is at the end of August in the French species and goes on till October. The sexual forms do not all leave the nest with the swarm, and the individuals that remain behind keep their wings for a very long time. Grassé has shown that in *Calotermes* there are sexual forms that have lost their wings, but whose gonads may still be even less matured than those of the soldiers. He gives the name ‘*achrestogonimous forms*’ to these individuals, which play no useful part in the life of the

Fig. 118 – A soldier of *Neotermes aburiensis* (Protermitidae), from West Africa (after GRASSÉ).

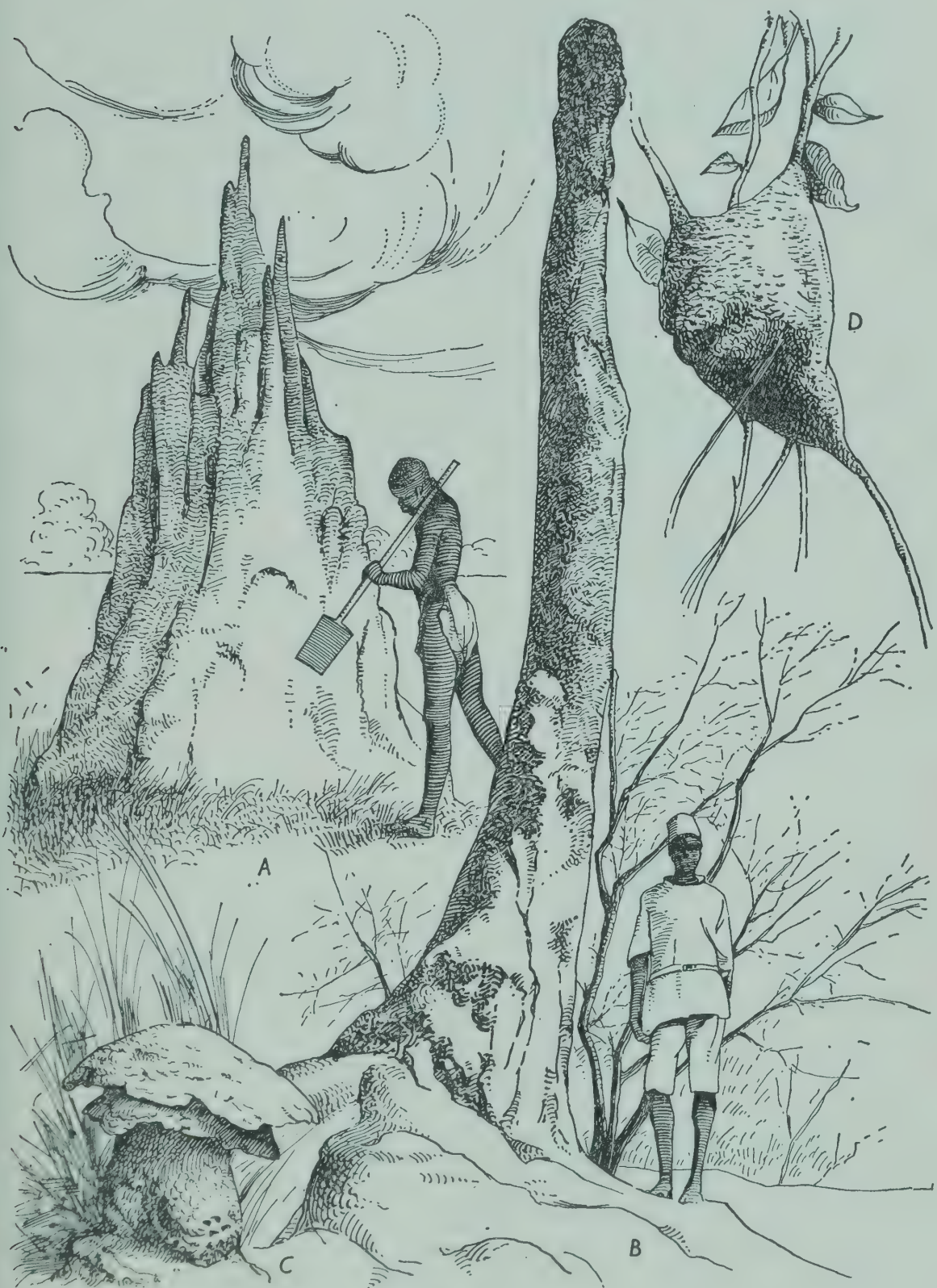


colony (Fig. 119). They may belong to the colony, or they may perhaps be intruders from a strange nest, which have been tolerated, but given a diet which did not allow them to mature. On the other hand it has been

PLATE 2 – IX. NESTS OF ANTS AND TERMITES

- A. A pinnacled termitarium of **Bellicositermes natalensis**, in southern Africa (after HEGH).
- B. Termitarium of **Bellicositermes jeanneli** in the vicinity of Lake Rudolph. Some of them reach a height of 10 metres.
- C. A mushroom-shaped nest of **Cubitermes** in West Africa. (after HEGH).
- D. An aerial nest of an ant: **Crematogaster stadelmanni** var. **dolichocephala**, from the Congo (after HEGH).

PLATE 2-IX. NESTS OF ANTS AND TERMITES



proved experimentally that winged sexual forms that remain behind in the nest are capable of pairing off on the spot, without swarming, and becoming additional royal couples.

MESOTERMITIDAE. These are more highly evolved than the last group, and have workers as well as soldiers of several sizes (Fig. 120). The nests are made in dead wood and are not concentrated. *Leucotermes lucifugus*

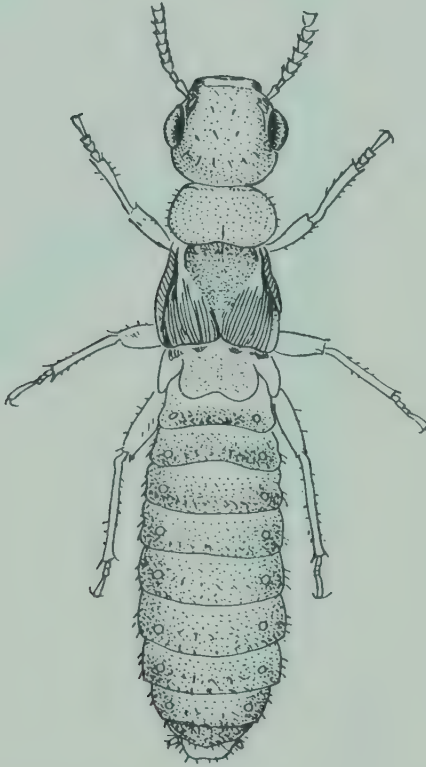


Fig. 119 - An achrestogonimous female of *Cryptotermes lamanianus* (Protermitidae), from the Ivory Coast (after GRASSÉ).

does serious damage to the woodwork of buildings in south-western France. Grassé has described the architecture of a nest of *Schedorhinotermes* in an old trunk of *Bombax* in West Africa (Fig. 121). It consisted of an irregular arrangement of cells of varying sizes, made of a thin paper of wood-pulp. Near the middle was a chamber the size and shape of an olive, which was empty, but which must have been the royal chamber.

The soldiers of this species squirt out from a frontal pore an evil-smelling liquid as a means of defence. When Grassé had broken open the nest he observed how the bulk of the population moved down into the lower part of the nest. The workers and the soldiers seized the immature forms and removed them into the deepest cells. The soldiers of *Coptotermes* can also squirt out a defensive fluid that is milky in texture, like latex.

METATERMITIDAE. This group is the most numerous and the most highly evolved, and is referred to as the 'higher termites'. The castes are highly developed, workers and soldiers, big, middle-sized and small (Fig. 122), each kind having a more or less distinctive part to play in the life of the colony. The nests of this group of termites are concentrated,

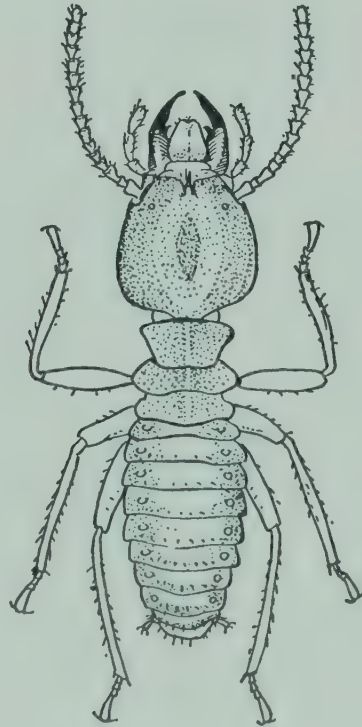
and vary in type. Some are aerial, built in trees; others are subterranean, and are solid structures of a characteristic style in each species.

Cubitermes builds its nests on the trunks of trees in the form of a ring from which covered galleries run down to the ground. These nests are made from an earthen cement that is black and very hard, and inside are horizontal groups of cells. Other species, like those of *Microcerotermes*, build paper nests in globular shape, placed in the forks of trees, and popularly known as 'têtes de nègres'. In all kinds of arboreal nests of termites the royal cell is to be found at the centre of a number of communicating cells, in which the brood is reared.

Very different are the many kinds of nest built up from ground level by a variety of species of METATERMITIDAE. Their external appearance varies a good deal, but they fall into two categories, those which do not build fungus gardens, and those which have them. Grassé (1937), *Annales de la Société entomologique de France*) has given a detailed description of the termitarium of *Bellicositermes natalensis* and *B. bellicosus* in West Africa, and that description is applicable to all the termites that cultivate fungi.

The termitarium is constructed from earth, and is generally cone-shaped (Fig. 123). in *B. natalensis* it scarcely exceeds a height of four

Fig. 120 - A big soldier of *Schedorhinotermes provisorius* (Mesotermitidae), from West Africa (after GRASSÉ).



metres. The outer wall is very thick, and consists of earth mixed with sand and clay, and made into a cement with saliva. A network of galleries lies inside the outer wall, which has no opening to the exterior. The

mound becomes broader at the base, where it encloses the living-chamber, the place where the royal cell and the fungus gardens are to be found. There is a space, sometimes considerable, between the living-chamber and the outer wall.

The living-chamber rests on a platform supported by conical pillars, with their points downwards into the soil. The platform is a little below

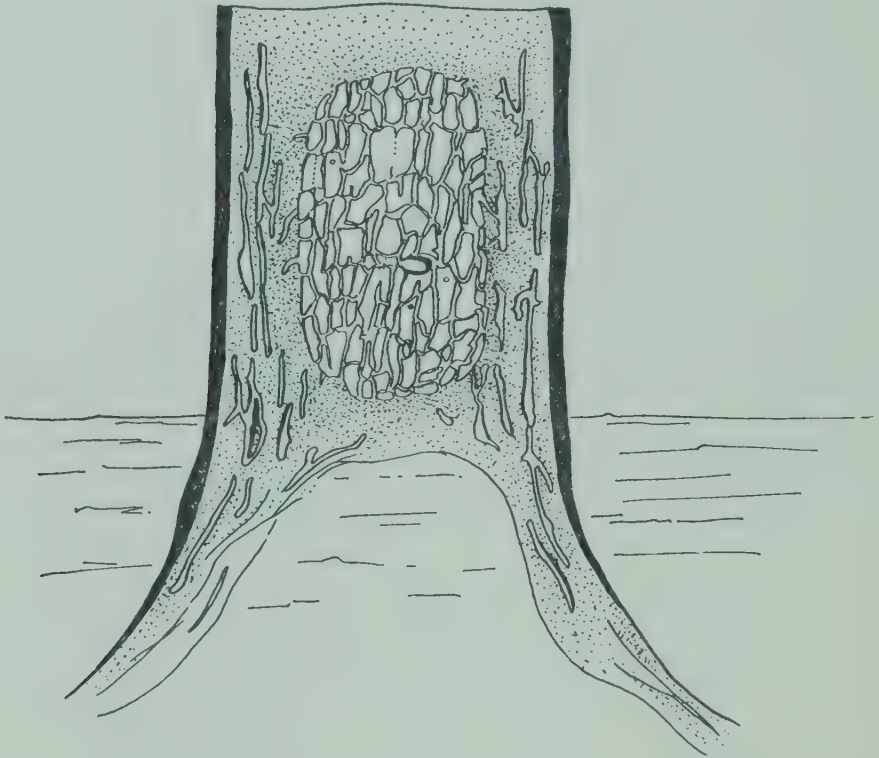


Fig. 121 – Nest of *Schedorhinotermes provisorius* (Mesotermitidae), built in an old trunk of *Bombax*, on the Ivory Coast (after GRASSÉ).

the surface of the ground, and on it stands a complicated superstructure which houses the royal cell and the fungus gardens.

The termites go a long way to get building materials. They build the arches of the living-chamber out of drops of faecal paste (Fig. 124), and it is astonishing that teams of blind workers, each building independently, can construct segments of arches so regular that they come together and meet exactly.

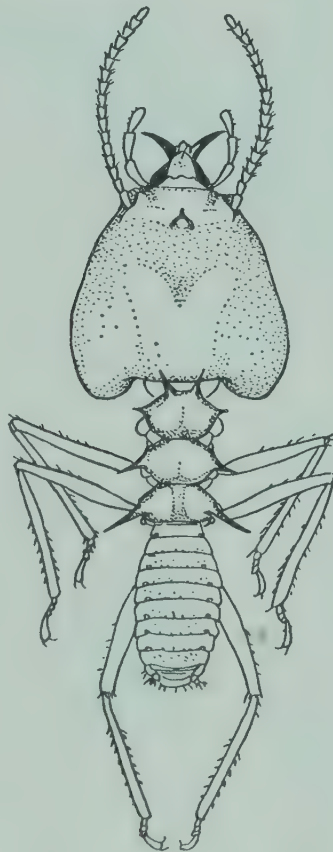
The *royal cell*, Pl. 2, X (A), is to be found near the middle of the living-chamber. Its floor is flat and thin, and has a big cavity below it, while over it is a low vaulted roof, which shelters the royal couple. Attendant workers feed them, and carry away the eggs that are laid at the rate of tens of thousands a day. It has been shown that the famous reconstruction by Escherich, in which the workers danced round the queen, while soldiers guarded her, has no basis in fact.

The structures known as *fungus gardens*, Pl. 2, X (B, C), have been well

known for a long time. These are more or less spherical, rather like sponges, lying free in some of the lower cells of the living-chamber. For a long time it was thought that the termites sowed and cultivated fungi in these gardens in order to feed on their fruiting bodies, but it is now known that this is not true, Pl. 2, X (D). There are no fungus-growing termites to correspond to the ant *Atta* that we have mentioned above. The sponge-like objects are built as shelters for the young of the termites, in which they can find a constant temperature and humidity. The observations of Grassé, a zoologist, and of Heim, a botanist, have shown that the fungus is an unwanted parasite, which grows in the favourable environment, quite independently of any action by the termites.

Bellicositermes collects fragments of wood, and other species (*Macrotermes*) return in procession to the nest carrying pieces of leaf in the same way as the American Parasol Ants (*Atta*). These fragments are piled up in the upper cells of the living-chamber, like a heap of sawdust, which the workers masticate with saliva. After it has dried, this material is used again to make the sponge-like structures, apparently by eating it and

Fig. 122 – A big soldier of *Acanthotermes acanthothorax* (Metatermitidae), from the Ivory Coast (after GRASSÉ).



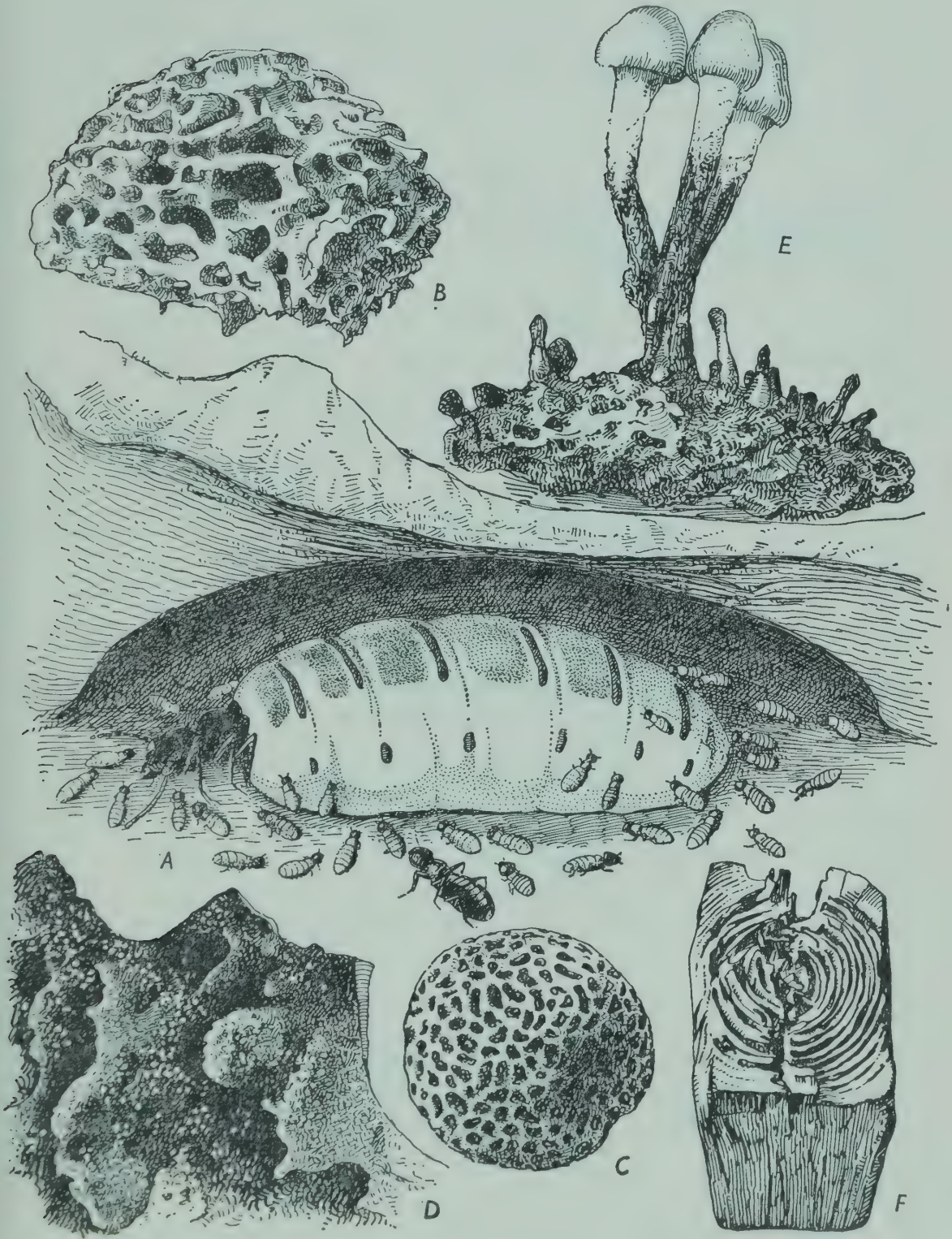
passing it out as faecal pellets, of which traces can be seen in the final construction.

The fungus concerned is an Agaric, and gives the sponge-like structures a velvety appearance. The fruiting-bodies are used only as an occasional

PLATE 2-X. TERMITES

- A. The Royal Cell of **Bellicositermes bellicosus**. The queen has the king close to her, and is surrounded by workers, who groom her and lick her exudations.
- B. A fungus-garden of an African termite (**Odontotermes latericus**) (after HEGH).
- C. A fungus-garden of **Termes minutus** in the Ivory Coast (after HEGH).
- D. Fragment of a fungus-garden, showing the fungus heads (after HEGH).
- E. Agarics growing on a fungus-garden of **Termes redemani** (after HEGH).
- F. Damage to a piece of wood, caused by termites: the soft tissues of the wood have been eaten (after HEGH).

PLATE 2-X. TERMITES



or supplementary food by the termites. Under certain conditions the fungus may grow a large head, which may penetrate the outer wall of the termitarium and break out into the open air. Pl. 2, X (E). The termites know the danger of this, and take action to get rid of the fungus when it begins to grow big. In this respect they treat it just like a harmful commensal animal.

Termitophilous Insects

More than 500 species are known to live as commensals in termites' nests, though this is fewer than the commensals of ants. Coleoptera

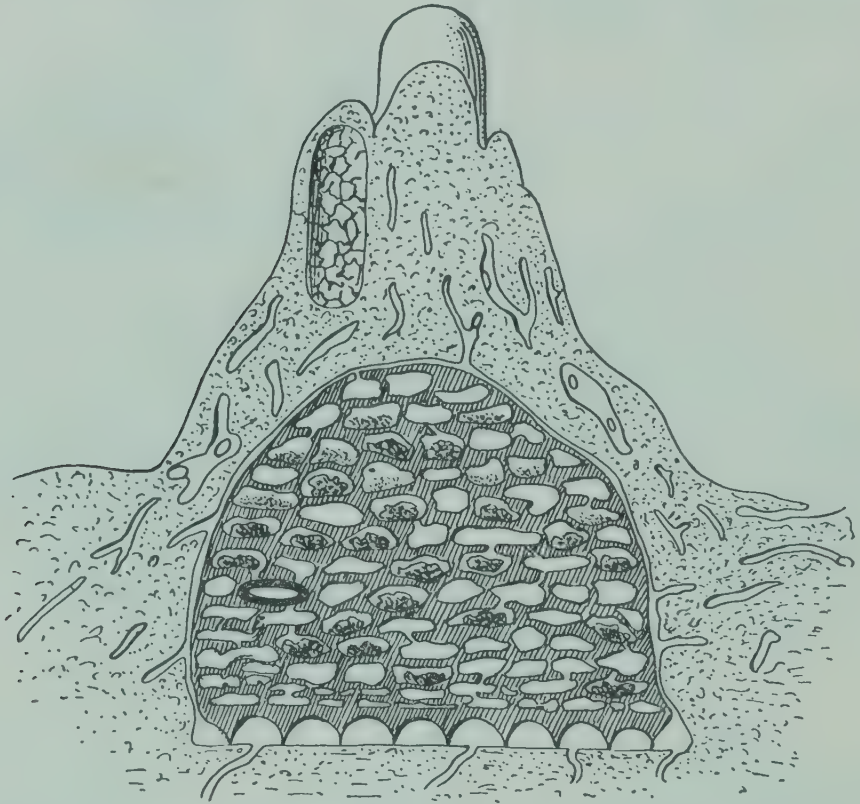


Fig. 123 – Nest of *Bellicositermes natalensis* (Metatermitidae), from the Ivory Coast (after GRASSÉ). The thick outer wall is riddled with galleries; above, on the left is a newly-built section. The living chamber, resting on arches, consists of many cells, some of which contain the sponge-like structures associated with the fungus-gardens. The royal cell, shown circled in black is to the left of the middle.

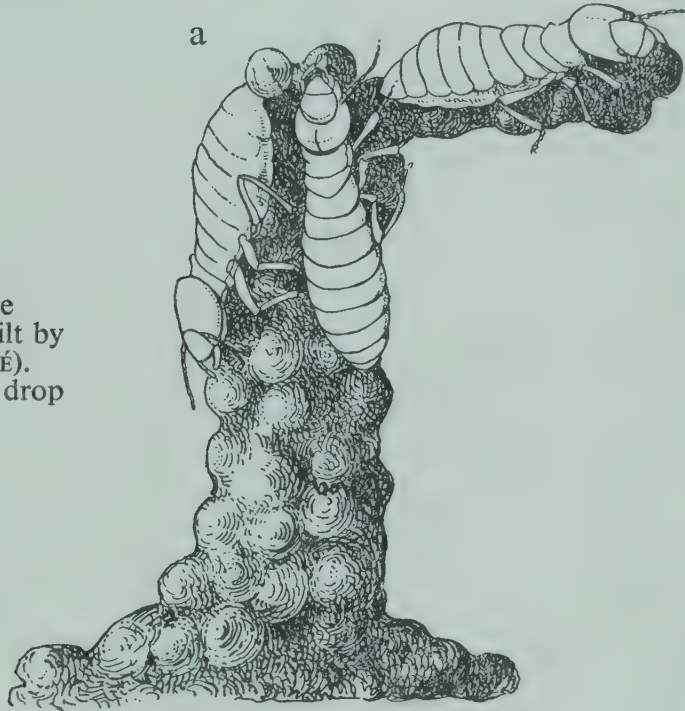
mainly STAPHYLINIDAE, are in the majority, but there are also Diptera of extraordinary shape, caterpillars of Lepidoptera, Orthoptera, Thysanura, Collembola, and even Arachnids and worms. In their relations with the host they can be classified in much the same way as the commensals of ants

There are synoeketes which are just tolerated, like Orthoptera or

Collembola. There are also true synechthrans, like the big Carabid beetles of the genera *Glyptus*, *Orthogonius* and others, whose larvae dig pits near the galleries and lie in wait to catch and eat the termites.

The most remarkable of the termitophiles are the symphiles, which are looked after and sought after by the termites because they have trichomes. These commensals have a characteristic that is particularly

Fig. 124 – An arch of the living-chamber being built by the termites (after GRASSÉ). Termite (a) is exuding a drop of faecal paste.



associated with termitaria, the swelling of the abdomen known as *physogastry*. The flies and some of the Staphylinids have the abdomen of a monstrous size, so bloated and deformed that it comes to be folded over the top of the head and thorax, and may hide them completely. The most extraordinary in this respect are the fly *Termitoxenia* and the beetle *Corotoca* (Fig. 125).

The term ‘physogastry’ is misleading, since it means ‘with the stomach inflated with air’. The distension of the termitophiles is due to the excessive accumulation of fatty materials in over-fed individuals: it is an obesity. In fact the termites feed their symphiles like a bird feeding its young, and the distension of the abdomen is comparable to the way in which the honey-ants stuff certain of their workers and make honey-pots out of them.

Moreover, not all Staphylinids and Diptera in the termitarium become physogastric. There are some, like *Termitodiscus* and *Thaumatoxena*, which take on a disc-like shape and have thickened, short limbs that can be withdrawn beneath the carapace, doubtless in order to avoid the mandibles of the soldier termites.

Finally, the termitarium provides remarkable examples of complex biocenoses. Very small termites (*Microtermes*) set up their nests within the nests of some of the bigger species, and live there as kleptoparasites.

It may be added that the *outside* of a termitarium has its own special fauna and flora. Some plants prefer to grow there, and there are Cicindelid beetles whose larvae dig their traps in the walls of termitaria in Ceylon.

Enemies of Termites

In some tropical areas termites are so abundant that one might say that they are masters of the country. Yet they have many enemies, even if these are not able to keep the termites in check.

All kinds of vertebrates feed on termites, whether they look for them actively in the termitarium, like the Pangolins and Anteaters of Africa, or just go after them at the time of swarming. Birds, lizards, chameleons, geckoes, mammals great and small, even men, combine to destroy millions of them. But perhaps the greatest enemy of termites is the ant, certain species of which wage constant war on them. The DORYLINAE and PONERINAE periodically wipe out termite colonies.

In Africa *Megaponera foetens*, which is known as the 'Corpse Ant' because of its abominable smell, makes concerted raids on termitaria. They set out in long columns, two abreast, break into the termitarium, and start a furious fight. After a certain time they march out again in good order, and return to their own nest, almost always carrying in their mandibles worker and soldier termites, immersed in saliva. The



Fig. 125 – *Paracorotoca akermanni*, a Staphylinid beetle that lives in termites' nests, and is physogastric (after WARRENS).

cripples, following painfully in the rear, testify to the fierceness of the fight, while the fact that I have seen a member of a column of *Megaponera* victoriously carrying off a king termite shows that the raiding party had been able to penetrate right to the royal cell.

Part Three

PALAEONTOLOGY AND GEOGRAPHICAL
DISTRIBUTION

9

The Evolution of Insects

THE insects are the most ancient inhabitants of the continental masses. They have left fossil remains from the Devonian onwards, and the state of evolution that they had then already reached shows that they must have branched off in the Silurian, at the latest. Ever since terrestrial animals appeared on Earth, insects have multiplied in all kinds of environment.

The oldest known insects do not differ fundamentally from those of the present day. The Palaeozoic insects had the same organs as those of living forms, but in a more primitive state. We must therefore start by explaining just what we mean when we say that an organ is 'primitive'.

In a primitive organism the various parts of the body are very much alike, and show a comparable state of development: they are said to be 'homodynamic'. Thus, in the Palaeozoic insects all the segments of the abdomen are alike, and so are the three pairs of legs, while the wings have a large number of very similar veins. In the course of time, the emergence of evolutionary lines is marked by the *specialization* of different parts of the body. Some become more important, and more complicated, in association with some function that they perform; others become smaller, and tend to disappear. Along each evolutionary line these changes tend to lead in a particular direction, a phenomenon known as 'orthogenesis'.

Evolution is irreversible. Once an organism has started to specialize thus orthogenetically it has to go on, and can never turn back to what it was before. An organ that has begun to specialize must specialize more and more, and at the same time automatically makes itself less and less able to perform any other function. This progressive specialization means that as a group of animals evolves it becomes more and more dependent on the continued existence of the particular environment for which it is adapted. When in due course conditions change, a highly specialized line is doomed to extinction.

Palaeontology teaches us graphically that an evolutionary line has a limited existence. It appears, specializes more and more, and then after a period of time that may be long or short, on the geological scale, it eventually becomes extinct. In short, it has a life: it is born; it blossoms out: then it dies, and gives place to another.

Insects are not immune from this law. Just as the biological stage has been dominated in turn by successive groups of vertebrates, each

more advanced than the last, so the various groups of insects have followed each other in the fossil record. We can watch how successive groups blossom out, flourish for a time and then eventually disappear, always abruptly, to be replaced by the new groups that are appearing on the scene.

Evolution thus progresses by stages. An evolutionary line passes through a phase of great plasticity, or variability, in which all kinds of new characters make their appearance. Some of these are a hindrance to the animal, some are of positive benefit, and some are neither. The problems of existence are met by a great multitude of different solutions, but nearly all of these come to nothing because the adaptation is not good enough to do its job efficiently. The fossil remains of extinct species provide innumerable examples of this. Once in a thousand times, or even more rarely, a happy combination of circumstances leads to a really efficient adaptation, which gives new vitality to the stock. A new line is launched, which goes out to conquer the world.

The insects provide striking examples of this groping method of evolution. How many of the fossil forms that we know about are misfires of this kind, ill-adapted, doomed from the start to disappear without leaving any descendants? The Protohemipteron *Eugereon*, the 'Bug-nosed Dragonfly' and the genus *Gerarus* of the Protorthoptera, with disproportionately long neck. Pl. 3, IV (A) and Pl. 3, IX (E and F), are very probably unsuccessful groups of this kind.

Insects, too, provide many examples of the temporary blossoming out of a group. In the Carboniferous the Palaeodictyoptera and the cockroaches flourished; the Planipennia and the Phasmids swarmed in the Jurassic.

The big climatic changes that came about at the end of the Palaeozoic period caused the rapid disappearance of most of the Permo-Carboniferous groups in the northern hemisphere. These stocks, already more than a hundred million years old, no longer had the power of adapting themselves to changed conditions. As we shall see, the Permian groups arose out of groups of the Carboniferous, and in their turn were replaced by the Mesozoic groups. The same story will repeat itself for the Odonata, for the Ephemeroptera, the Perloidea, and the Orthoptera: in fact for all the groups that have their origin in Palaeozoic times.

THE ANTIQUITY OF THE INSECTS

Today we have the means of estimating in millions of years the immense period of evolution of the insects. Geology has found a new time-scale in radio-activity, and a new science of radiogeology is devoted to measuring the age of rocks, and simultaneously that of the fossils they contain. The method consists of estimating the products of the decay of

the radio-active materials in the rocks, the quantity of which is a function of the length of time that has elapsed since the rocks were laid down. The age of sedimentary rocks can be worked out like this in millions of years, with a margin of error that is not greater than 20 per cent. This is an unforeseen consequence of the work of Henri Becquerel and Pierre Curie in atomic physics, to have put new life into geology in this way, by giving it a new method of measuring the lapse of time.

The most ancient rocks that are known are at least three thousand million years old. They are the Precambrian pegmatites of Southern Rhodesia. The earliest fossil-bearing rocks of the Cambrian date back only about 500 million years. We can feel confident that at least 440 million years have gone by since the first insects emerged from a marine stock and populated the lands—that had likewise emerged from the sea.

It is hard to know whether to marvel at the length or at the shortness of the geological time that has served for the evolution of the terrestrial fauna and flora. In any case, the figures arrived at by radiogeology agree with the conclusions of astronomy.

One fact that emerges from the table of the geological periods that is given later on pages 237-9 is the relative length of the various periods of the Palaeozoic era. The beginning of the Carboniferous was 270,000,000 years ago, but this is just about the middle of the time from the start of the Cambrian to the present day. This should be borne in mind when considering the problem of the origin of the very rich fauna of winged insects that appeared in the coal measures.

In a general view, therefore, the Insects must be looked on as very ancient. They are twice as old as the Reptiles, which are old inhabitants of the Earth, and three times as old as the Mammals: perhaps a thousand times as old as the human species.

Having obtained some idea of the time that has lapsed since the first insects appeared on the scene, we may ask at the same time where this event took place. Some think that stocks of primitive insects came into being in different countries, independently of one another: others are inclined to suppose the insects to be monophyletic, having arisen only once, at some point where conditions were especially favourable. Without being able to prove it, we ourselves think it is probable that the first insects arose from a marine stock on some marshy shore of the tropical Silurian continents, no doubt on the edge of the ancient asylum of Laurentia, which we shall discuss later. Since the evolution of the insects unfolded, in the course of time, alongside that of the plants, it seems natural to assume that their origin, too, was linked with that of the terrestrial vegetation.

THE MAJOR LAND-MASSSES, OR ASYLUMS¹

To get a fair idea of the evolution of the insect fauna we have to consider, first of all, the broad outlines of the changes that have taken place in the geography of the Earth since the beginning of the Palaeozoic.

The famous Viennese geologist E. Suess was the first to elucidate clearly the part that is played in the evolution of living organisms by the *asylums*, or land-masses that are particularly stable and are characterized by the absence of evidence of recent folding, and the rarity with which they are



Fig. 126 – The three great land areas, or ‘asylums’, during the Carboniferous (after ARDLT).

invaded by the sea. It was on these asylums, protected from inundation by the sea, that the terrestrial faunas had their origin; there they began their evolution, before spreading over the Earth in a succession of migratory movements.

The three major land-masses that formed the cradles of the insect fauna were *Laurentia*, *Angara Land* and *Gondwanaland* (Figs. 126 and 127).

Laurentia corresponds to the stable region known to geologists as the ‘Canadian shield’, which has no marine deposits later than the Cambrian. From the view-point of the biogeographer the Laurentia of the geologists must be augmented by also including all the mountain-chains that have arisen round its borders, that is the Caledonian and Hercynian foldings that have prolonged the Canadian shield eastwards, through Greenland, the British Isles, Scandinavia and Western Europe. At certain periods these European outposts have extended even farther eastwards, up to the Russian platform, so that we could consider the eastern limit of the Laurentian asylum as the shores of the sea that nearly always existed in

¹ TRANSLATOR’S NOTE. This term was first proposed by E. Suess, and appears in the ‘authorized English translation’ of his book *Das Antlitz der Erde* (1909, vol. iv, p. 660): ‘Places of refuge . . . we shall term them therefore *asylums*.’ The French term used by Dr. Jeannel in the present work is ‘*asiles*’.

the Ural region. These seas, which for long periods have linked the Arctic with the early Mediterranean, separated the European part of Laurentia from another land-mass farther east, known as Angara.

Angara Land gets its name from the river Angara, or upper Tunguska, that flows out of Lake Baikal and joins the Yenisei. The Siberian Platform, whence flows the Angara, and sloping down to the Arctic Ocean in the north, constitutes one vast *asylum*, never covered by the sea since

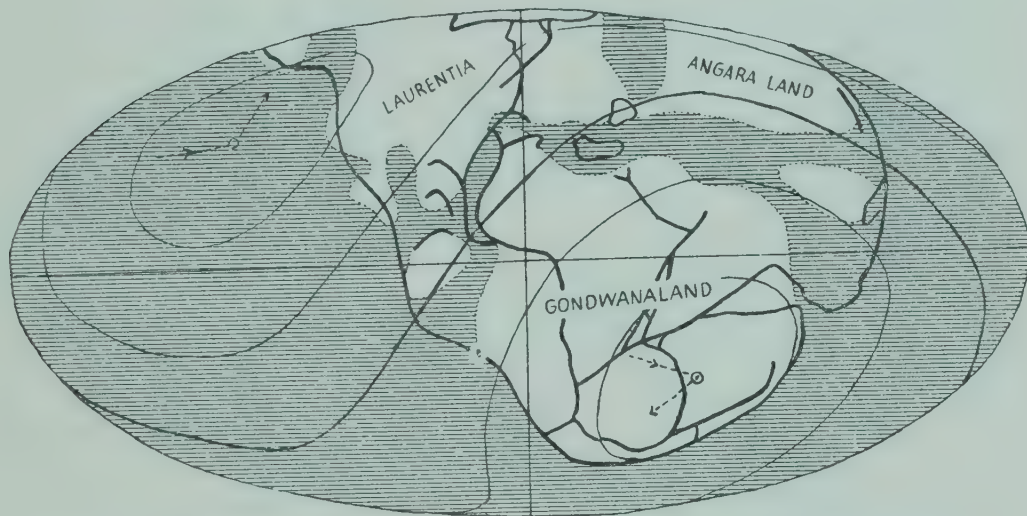


Fig. 127 – The three ‘asylums’ of the Carboniferous, with the continents bunched together in accordance with WEGENER’s theory.

Cambrian times. Great ranges of mountains have arisen on its southern border, and these are the heart of Angara.

Gondwanaland is the great land-mass of the Southern Hemisphere. In Palaeozoic times Gondwanaland was enormous, but in the Mesozoic Period it became broken up so that its scattered remains are to be found in the present-day Brazil, Africa and Arabia, Madagascar, the Indian Peninsula, Australia and New Zealand, and Antarctica. The name ‘Gondwanaland’, given to it by Suess, is that of an area of the Central Provinces of India, where there is the most complete series of the strata which bear the so-called ‘*Glossopteris*-flora’, characteristic of all the fragments of Gondwanaland.

As we can see, two of the asylums were located in the Northern Hemisphere, and the other, Gondwanaland, in the Southern. In every geological period Gondwanaland has been separated from the northern asylums by a great marine barrier, the primitive Mediterranean (*Tethys*) extending from the Antilles to Malaya. There have been temporary interruptions in the continuity of this marine barrier during periods when the oceans have receded (*geocratic periods*), which have made possible an interchange of fauna and flora between the three asylums.

PLATE 3-I. A FOREST OF THE UPPER
CARBONIFEROUS PERIOD IN LAURENTIA

Lepidodendraceae and Sigillariaceae (on left)

Horse-tails and Club-mosses (on right)

Arborescent Pteridosperms (in background).

A marshy tropical forest, in which lived *Palaeodictyoptera*,
and other insects of the Upper Carboniferous.

(Reconstructed by PAUL BERTRAND)

PLATE 3-I. A FOREST OF THE UPPER
CARBONIFEROUS PERIOD IN LAURENTIA



Within these asylums, which are in effect the three permanent continents of the Earth, the climate has varied from one period to another. There is no doubt that in all the geological periods the climates of the Earth have been distributed in relation to the poles, as they are today. In every period the poles have been glaciated, and the equatorial belt hot, and all the evidence from palaeoclimatology indicates that within each zone the mean temperature was roughly the same as it is today. What has taken place is a migration of the poles, which has shifted the whole pattern of climatic zones about the Earth, from one period to another.

Whether one adopts Wegener's theory, which holds that the continents were joined together during the Palaeozoic and later drifted apart, or whether one believes that the nuclei of the continents have always been fixed, there is none the less one idea that it is impossible to reject: the migration of the poles. It cannot be disputed that the relative position of the continents to the poles has never ceased to change throughout geological time, and still does so.

The three asylums have been differently affected by the migration of the poles. Laurentia lay on the Equator in Carboniferous times (Pl. 3, I), but it gradually became colder during the Mesozoic and the Tertiary, till it became glaciated in the Quaternary. On the other hand Gondwanaland had the South Pole at its centre in the Carboniferous, and its progressive warming up during Mesozoic and Tertiary times is in opposite phase with the cooling of Laurentia. As for Angara Land, this land-mass has remained in a fairly constant relation to the poles, and its climate has remained temperate or subtropical, varying little.

We know that these climatic changes in the asylums must have had their repercussions in the movements of faunas, and big exchanges have taken place between Laurentia and Gondwanaland in all the geocratic periods, when the marine barrier between them has been broken down. Angara, on the other hand, has always been a refuge of conservative groups, especially throughout the Mesozoic.

The geological history of these great land-masses gives the key to the evolution of the various insect stocks. The following table lists the great geological periods, and their major divisions, without going into details of the various smaller zones. Wherever there is a well-defined continental facies the name of the Period is given in brackets (e.g. Trias, Permian, Carboniferous). Not all the deposits of fossil insects can be mentioned, and the list is confined to those which are discussed in this volume, and which are some of the more important.

THE GEOLOGICAL PERIODS

QUATERNARY ERA (Duration: 1 million years)

Quaternary (1 million years)	PLEISTOCENE	
	POST-PLIOCENE	

TERTIARY ERA (Duration: 20 million years)

Neogene (5 million years)	PLIOCENE	
	MIOCENE	<i>N. America: Florissant (Colorado)</i>
Nummulitic (15 million years)	OLIGOCENE	<i>Europe: Baltic amber; Caylux phosphates; Aix-en-Provence</i>
	EOCENE	<i>Europe: Monte Bolca (Italy)</i>
	MONTIAN	

SECONDARY ERA (Duration: 160 million years)

Cretaceous (60 million years)	UPPER	
	MIDDLE	<i>Europe: Bohemia (first Angiosperms)</i>
	LOWER	
Jurassic (60 million years)	UPPER	<i>Europe: Lithographic limestone of Solenhofen (Bavaria)</i>
	MIDDLE	
	LOWER (Lias)	<i>Asia: Shurab (Ferghana); Galkino (Eastern Siberia)</i> <i>Europe: Mecklenburg; England</i>

Trias (40 million years)	UPPER (Keuper)	<i>Australia: Ipswich (Queensland)</i>
	MIDDLE (Muschelkalk)	
	LOWER (Variegated sandstone)	

PRIMARY ERA
(Duration: 310 million years)

Permian (30 million years)	UPPER (Thuringian)	<i>Australia: Belmont, Newcastle, N.S.W.</i> <i>Russia: Kargal (Orenburg); Tikhia Gory (Kazan); Iva Gora (Archangel)</i>
	MIDDLE (Saxonian)	
	LOWER (Autunian)	<i>N. America: Elmo (Kansas)</i> <i>Europe: Birkenfeld (Thuringia)</i>
Carboniferous (60 million years)	UPPER (Stephanian)	<i>Europe: Commentry (Allier)</i>
	MIDDLE (Westphalian)	<i>N. America: Mazon Creek (Illinois)</i> <i>Europe: Lens, Liévin, Bruay, Anzin</i>
	LOWER (Dinantian)	<i>N. America: Fayetteville (Alabama)</i>
Devonian (80 million years)	UPPER	
	MIDDLE	<i>Europe: Peat Moss of Rhynie (Scotland)</i>
	LOWER	

Silurian (80 million years)		First scorpions
Cambrian (60 million years)		

PRECAMBRIAN ERA
(Duration: 2,000 million years)

Algonkian		
Archaean		

THE MAJOR GROUPS OF PTERYGOTE INSECTS

In order to make it easier to understand what follows it may be helpful to recall at this point that the thirty-six Orders of the Sub-Class *Pterygota* are grouped into four major categories. (See Chapter 5.) Their salient characteristics are as follows:

A. Section **Palaeoptera**—Wings held out flat when at rest. No jugal field in the wing. *Heterometabola*.

(Superorders Palaeodictyoptera, Ephemeroptera and Odonoptera.)

B. Section **Polyneoptera**—Wings folded backwards when at rest. Jugal field of the wing highly developed, with a multitude of veins. *Heterometabola*.

(Superorders Blattopteroidea, Orthopteroidea, Dermapteropteroidea.)

C. Section **Oligoneoptera**—Wings folded backwards when at rest. Jugal field of the wings specialized by reduction into a single, unbranched vein. *Holometabola*.

(Superorders Coleopteroidea, Neuropteroidea, Mecopteroidea, Aphanipteroidea and Hymenopteroidea.)

D. Section **Paraneoptera**—Wings folded backwards when at rest. Jugal field of the wing specialized by reduction into a single vein with branches. *Heterometabola*.

(Superorders Thysanopteroidea and Hemipteroidea.)

10

The Fossil Insects

Sub-Class *COLLEMBOLA*

1. **Order Collembola.** The Collembola are the most primitive of all insects, and the only ones with the protomorphous type of development. They are also the group that appears in the oldest geological deposits, and are known from the Devonian.

Remains of insects and of arachnids have been found in the great fossil peat-bog of Rhynie, in the north of Scotland. These tiny imprints in the Old Red Sandstone (Middle Devonian) had been known since 1926, but their authenticity was not accepted until 1940, after new research by Scourfield. The insects prove to be Collembola, and Scourfield has been able to show that their characteristics do not correspond exactly with any of the families that exist today. In their antennae they resemble *PODURIDAE*, but the absence of a distinct prothoracic tergum links them with the *Entomobryidae*. They are provisionally placed in the following family:

Family *PROTENTOMOBRYIDAE* Folsom. *Rhyniella praecursor* Hirst and Maulik had already a jumping apparatus ('spring') as highly developed as that of living Collembola. There are hardly any indications of the structure of the furca, but certain fossil imprints have shown clear traces of a ventral tube and of a retinaculum, appendages of the first and third urites.

Tillyard has drawn attention to the significance of the antennae of *Rhyniella*, which apparently represent a most primitive form, from which can be derived all the multi-segmented antennae found among the insects. The primitive antenna has only three segments: scape, pedicel and flagellum—but the flagellum shows an annular furrow which foreshadows the further segmentation. This leads us to the four-segmented antenna of living Collembola, and which is also found in the larvae of very many groups of insects.

Apart from the antennae, *Rhyniella praecursor* of the Middle Devonian appears on the scene equipped with all the evolutionary characteristics of the recent Collembola. We must infer from this that the stock must have already been an old one in Devonian times, and must have existed for millions of years before its appearance in the Rhynie Bog.

The family *PROTENTOMOBRYIDAE* was founded by Folsom for his own *Protentomobrya walkeri*, of the Cretaceous of Canada, which recalls

Rhyniella, and which could have been a later descendant of the same stock.

A variety of fossil Collembola are known from the Tertiary deposits, but these belong to families that still exist today. There are beautiful specimens in the Baltic Amber.

Sub-Class *PROTURA*

2. Order **Protura**. These minute insects are not known as fossils. The living members of the Order have only recently been discovered.

Sub-Class *THYSANURA*

No Thysanura are known from the early geological eras. Ch. Brongniart thought that he had found Thysanura in the Upper Carboniferous of Commeny, but his *Dasyleptus lucasi* is only a fragment of an arachnid or a crustacean. Nor is the Thysanuran described by Matthey from Carboniferous schists of St. John any more real.

It is strange that no authenticated remains of any Thysanuran have been found in any of the Mesozoic deposits. The first recognizable species are those of the Baltic Amber of the Lower Oligocene.

3. Order **Entotropha**. Family CAMPODEIDAE Westwood. One species of the genus *Campodea* has been recorded from the Baltic Amber, but there are no known fossil remains of the families PROJAPYRIDAE or JAPYRIDAE.

4. Order **Ectotropha**. Family MACHILIDAE Grassi. Some species of the genera *Machilis* Latreille, *Praemachilis* Silv. and *Parastylus* Olf. are known from Amber; they differ from living species.

Family LEPISMATIDAE Esch. Several species from the Amber have been described by different authors. According to Silvestri these should be reduced to two only: *Lapropholis dubia* K. and B., which still exists, and *Lepidothrix pilifera* Menge, which has since become extinct (Fig. 128).

Sub-Class *PTERYGOTA*

A. SECTION PALAEOPTERA

Superorder PALAEODICTYOPTERA

This group flourished during the Carboniferous, and became extinct at the end of the Permian. It included the most primitive of the Palaeoptera, insects of great size, which held their wings out horizontally when at rest, like the dragonflies of the present day. Many of them had patterned wings, with transverse dark bands, or sometimes even with eye-spots.

The other characteristics of the group include: a small, rounded head, loosely articulated with the thorax; mouth orthognathous; compound

eyes and three frontal ocelli; antennae long, straight, multi-articulate, filiform; mouthparts generally of the chewing type, with mandibles short and strong, but nevertheless in certain groups the mouthparts became lengthened into a sort of beak, as in *Lycocercus*, Pl. 3, II (F); thoracic segments distinct and all alike; the three pairs of legs similar; tarsi three-segmented, as Handlirsch said they were, and not five-segmented, as Lameere believed; the last tarsal segment with two claws, and probably an invaginated empodium.

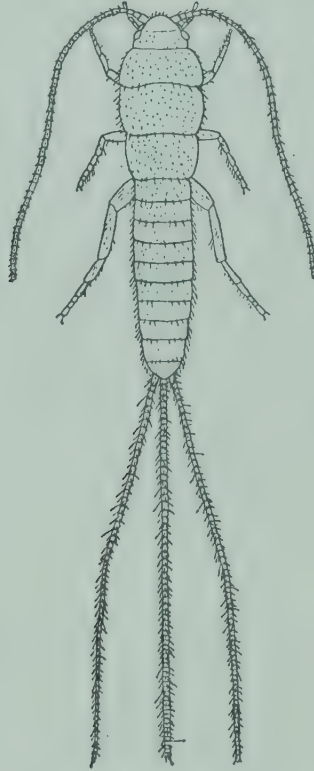


Fig. 128 - *Lepidothrix pilifera* Menge, a Thysanuran from the Baltic Amber (after HANDLIRSCH).

In the majority of the species of the Carboniferous, and many others of the Permian, the prothorax has fixed wing-pads, varying in shape, often striated, or ribbed, which are clearly rudiments of a pair of wings. The mesothoracic and metathoracic wings were similar to each other, long and straight, spread out in the horizontal plane, and not capable of being folded over the back, but moving up and down. All the veins were present and branched, with the branches curved backwards towards the hind-margin of the wing. Between the veins the wing-membrane was covered with an irregular network of polygonal areas (the *archedictyon*), which was highly developed in the primitive forms, but which in later forms first became simplified into a series of many transverse veins (*cross-veins*), and then became further specialized by reduction until only one or two were left.

The abdomen was long and broad, with eleven segments. The first ten were alike, and were provided with paranotal lobes, lateral extensions

that were homologous with the thoracic wings. These paranotal lobes were present in the most primitive species, but disappeared in the more advanced groups, such as the Protohymenoptera. The eleventh segment was small, and carried two multi-articulated and movable cerci. The genital armature was built up from two pairs of gonopods on the eighth and ninth segments, which in the females seem to have become a true ovipositor. *See* Pl. 3, II (F).

Early Stages. Fossil imprints of larvae are known (Pl. 3, II, Fig. A). They are said to have compound eyes, and rudiments of wings sticking out at right angles to the side of the body. These larvae were aquatic, and it seems likely that they underwent a great many moults in the water, before coming out as a subimago, to undergo a final moult on dry land, as the Ephemeroptera do today.

5. Order **Eupalaeodictyoptera**. These were Palaeodictyoptera of great size and ponderous shape, with short antennae and cerci: their wing-span was a minimum of 10–20 cm., and could be up to 50 cm. The wings varied in shape, but always had the basal part more or less enlarged, and never reduced, while the venation was complete, with either a well-developed archedictyon, or a multitude of cross-veins.

In the beginning they were probably saprophagous, but gradually became more and more specialized plant-feeders. The majority of the species had mouthparts of the chewing type, able to eat vegetable food, but some of them, such as the LYCOCERCIDAE and the LITHOMANTIDAE, had the mouth drawn out into a rudimentary proboscis.

All the known Eupalaeodictyoptera lived in the hot, humid forests of Laurentia during Carboniferous times. In the equatorial forests of the Westphalian period (Pl. 3, I) there were vast marshy areas occupied by Calamites, Lycopodiaceae and other aquatic or marshy plants. The larval insects lived in stagnant or running water, and the adults passed their lives flying heavily from one clump of vegetation to another in search of food, or to escape their enemies.

Very numerous and diverse throughout the Carboniferous, the Eupalaeodictyoptera disappeared from the Permian fauna, where they are represented only by three species from the Lower Permian of Kansas. The relative dryness of the Permian climate must have been responsible, if not for their total extinction, at least for their migration to other continents.

The Order Eupalaeodictyoptera is a very numerous one, with nearly two hundred species in twenty-four families. The greater number of these are only known from imprints of wings. According to Handlirsch the Eupalaeodictyoptera comprised all the '*Ur-Insekten*', the primitive stock from which all the various lines of Apterygote and Pterygote insects were derived. Lamcère rightly challenged this view, but he went too far when

PLATE 3 – II. PALAEODICTYOPTERA

A. A larval *Palaeodictyopteron*, twice natural size, from the Upper Carboniferous in England.

B. *Stenodictya lobata* BRONGN. (Stenodictyopteridae), two-thirds natural size, from the Upper Carboniferous of Commentry, Allier.

C. *Stilbocrocis heeri* GOLD. (Stenodictyopteridae), three-quarters natural size, from the Upper Carboniferous of the Rhineland.

D. *Mecynoptera splendida* HANDL. (Mecynopteridae), two-thirds natural size. Left fore-wing, from the Upper Carboniferous in Belgium.

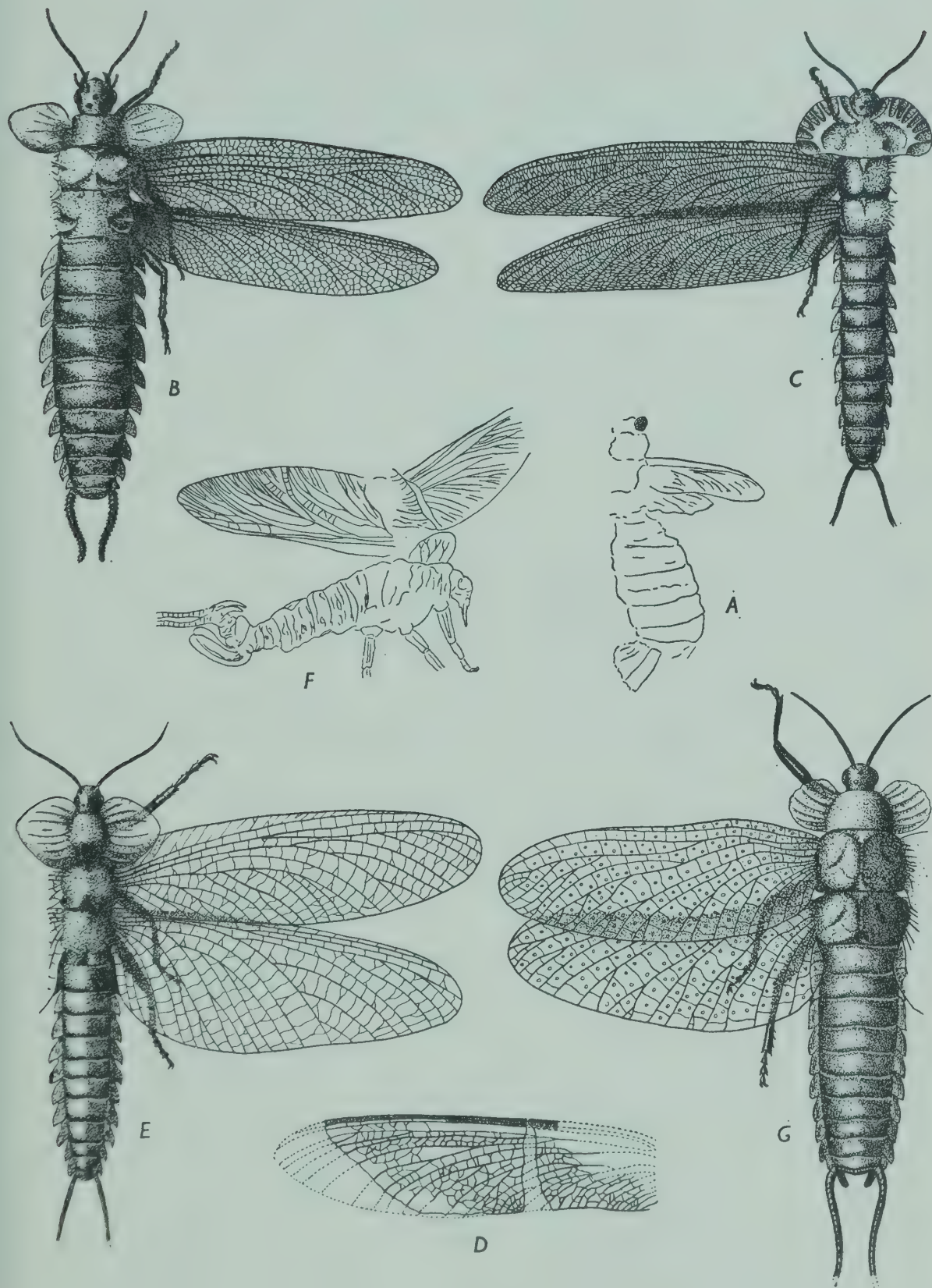
E. *Lithomantis carbonaria* WOODW. (Lithomantidae), two-thirds natural size, from the Upper Carboniferous of Scotland.

F. *Lycocercus goldenbergi* BRONGN. (Lycocercidae), one-half natural size, from the Upper Carboniferous of Commentry, Allier.

G. *Homoioptera woodwardi* BRONGN. (Homoiopteridae), one-half natural size, from the Upper Carboniferous of Commentry, Allier.

(After reconstructions by HANDLIRSCH).

PLATE 3 - II. PALAEODICTYOPTERA



he proposed to dismember the Palaeodictyoptera altogether, and to partition them between the Ephemeroptera and the Odonatoptera. All authors at the present time agree in retaining the Eupalaeodictyoptera as a group.

The principal families of the Order are as follows:

Family STENODICTYOPTERIDAE Brongniart (DICTYONEURIDAE Handlirsch). Insects of great size, and very robust. Prothoracic lobes, and paranotal lobes on the first ten abdominal segments. Wings long and parallel, the veins greatly branched, and the membrane covered with a very regular archedictyon.

Fifty species are known from the various Carboniferous faunas. They were dominant in the Westphalian of North America and Europe, and were still abundant in the Stephanian of Commentry, but by the end of the Carboniferous they were gone. Examples:

Stenodictya lobata Brongn., from Commentry. Pl. 3, II (B).

Stilbocrosis heeri Gold., from the Altenwald, in the Rhineland. Pl. 3, II (C).

Family MECYNOPTERIDAE Handlirsch. Differs from the preceding family in the less regular wing-venation, and in having a network of cross-veins in place of the archedictyon. A single species:

Mecynoptera splendida Handl. Pl. 3, II (D).

Family MEGAPTILIDAE Handlirsch. All the general characters are like those of the STENODICTYOPTERIDAE, but the wings are broadened at the base into a triangular shape like that of the BREYERIIDAE (*see below*). A single species:

Megaptilus blanchardi Brongn. Pl. 3, III (B).

Family LITHOMANTIDAE Handlirsch. Large size and robust build, with prothoracic lobes and paranotal lobes on the abdominal segments. Mouth-parts drawn out into a true beak. Wing-venation less complicated than that of the STENODICTYOPTERIDAE: no archedictyon, but many cross-veins that are delicate, and irregularly arranged.

Eight species are known from the Westphalian and Stephanian of France, England, Bohemia and North America. Example:

Lithomantis carbonaria Woodw., from Scotland. Pl. 3, II (E).

Family LYCOCERCIDAE Handlirsch. With the characters of the LITHOMANTIDAE, in particular with the same kind of snout, but without paranotal lobes on the abdomen. The imprint shown in the Plate clearly shows the leaflike gonopods of the female genitalia. Example:

Lycocercus goldenbergi Brongn., from the Stephanian of Commentry. Pl. 3, II (F).

Family HOMIOPTERIDAE Handlirsch. Big and ponderous forms, with broad, rounded wings. There are not many longitudinal veins, and the cross-veins mark out quadrilateral cells, each of which has one or two nodules, or papillae in it. There are also prothoracic wing-pads, paranotal lobes on the abdominal segments, and short cerci.

Four species in four genera, from the Stephanian of France and Belgium, are known. Example:

Homioptera woodwardi Brongn., from the Stephanian of Commentry. Pl. 3, II (G).

Family BREYERIIDAE Handlirsch. Characterized by the shape of the wings, which are short and broadly triangular, with few longitudinal veins and many cross-veins. Prothoracic wing-pads and paranotal lobes on the abdomen were evidently present.

Three species have been described from the Stephanian of France and Belgium. Example:

Breyeria borinensis Borre., from the Stephanian of Belgium. Pl. 3, III (A).

Family SPILAPTERIDAE Brongniart. A slender form, with very long cerci. Wings of varying shapes, but with the longitudinal veins much branched, linked by cross-veins that are thin, numerous and irregular. Prothoracic wing-pads and paranotal abdominal lobes may be present (*Homaloneura*) or absent (*Homaloneurina*).

The species of this family recall the Megasecoptera by their slender shape and long cerci. There are twenty species, in several genera, known from the Stephanian of Commentry. Three species have been found in the Lower Permian of Kansas, and these are the only Eupalaeodictyoptera that are known from deposits later than the Carboniferous. Examples:

Homaloneurina bonnieri Brongn., from the Stephanian of Commentry. Pl. 3, III (C).

Homaloneura ornata Brongn., from the Stephanian of Commentry. Pl. 3, III (D).

Family EUBLEPTIDAE Handlirsch. Very small insects, for this group, being scarcely 4 cm. in wing-span. Slender, with long cerci, but with neither prothoracic wing-pads nor abdominal paranotal lobes. The two pairs of wings are alike, and very much rounded at the tips, with few cross-veins. Eyes very big.

A single species, from the Upper Westphalian of North America, which is so extraordinary that one would be tempted to make a special Order for it.

Eubleptus danielsi Handl., from Mazon Creek, Illinois, is illustrated in Pl. 3, III (E).

PLATE 3 – III. PALAEODICTYOPTERA

A. **Breyeria borinensis** BORRE. (Breyeridae), fore-wing, natural size, from the Upper Carboniferous in Belgium.

B. **Megaptilus blanchardi** BRONGN. (Megaptilidae), fore-wing, natural size, from the Upper Carboniferous of Commentry, Allier.

C. **Homaloneurina bonnieri** BRONGN. (Spilapteridae), natural size, from the Upper Carboniferous of Commentry, Allier.

D. **Homaloneura ornata** BRONGN. (Spilapteridae), one-half natural size, from the Upper Carboniferous of Allier.

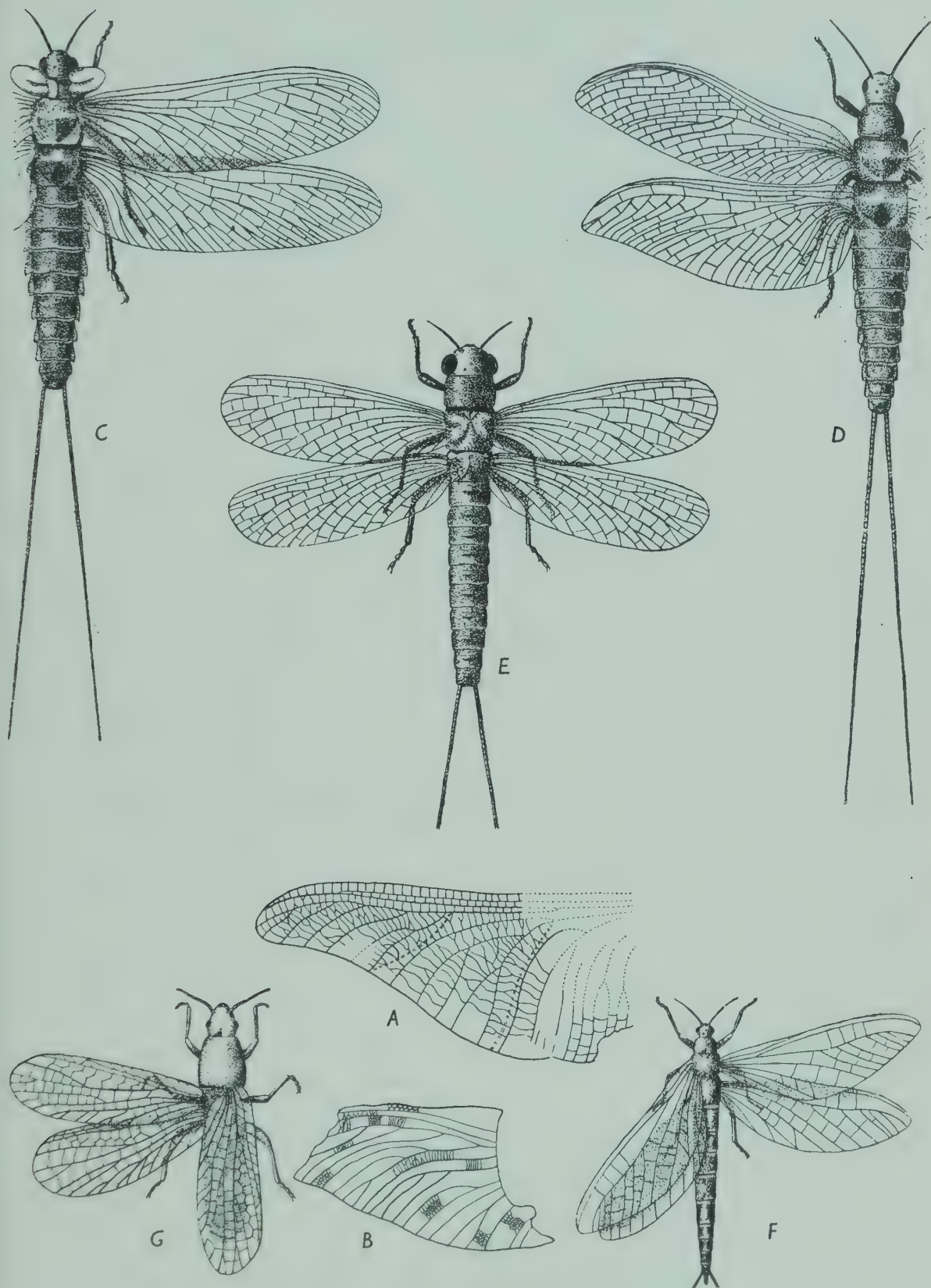
E. **Eubleptus danielsi** HANDL. (Eubleptidae), twice natural size, from the Middle Carboniferous of Mazon Creek, Illinois.

F. **Sypharoptera pneuma** HANDL. (Sypharopteroidea), twice natural size, from the Middle Carboniferous of Mazon Creek, Illinois.

G. **Hadentomum americanum** HANDL. (Hadentomoidea), natural size, from the Middle Carboniferous of Mazon Creek, Illinois.

(After reconstructions by HANDLIRSCH).

PLATE 3 - III. PALAEODICTYOPTERA



6. Order **Protohemiptera**. This Order was set up for a fossil insect that was at first thought to be ancestral to the Hemiptera, but which is now recognized as belonging to the Palaeodictyoptera, though it is remarkable for having the mouthparts modified in a way that resembles those of the Homoptera.

This 'Bug-nosed Dragonfly' had a small, elongate head, with small, prominent eyes. The mouthparts formed a snout, in which could be distinguished clearly a long, thin labrum, two pairs of stylets (mandibles and maxillae) ensheathed in a pair of five-segmented appendages formed from the labial palpi. This type of rostrum, the labial type, is much the same as that of the Hemiptera, but the resemblance should not be treated as any more than convergence.

This insect has, in fact, all the general characters of the Palaeodictyoptera. Its thoracic and abdominal segments are homonomous; there are prothoracic wing-pads, but no abdominal paranotal lobes. The wings, when at rest, were held out horizontally, at right angles to the body, and had a venation rather like that of the LITHOMANTIDAE, but with a well-preserved archdictyon. The legs were long and the tarsi three-segmented. There do not appear to have been any cerci.

Family EUGEREONIDAE Lameere. This family was erected for *Eugereon böckingi* Dohrn., a robust species, 6 cm. in wing-span, the imprint of which was found in the Lower Permian of Birkenfeld, in Germany. It seems as if Lameere was right when he grouped with this certain fossils from Commeny, *Mecynostoma* Brongn., *Mecynostomites* Handl., and *Paramecynostoma* Handl.: but the shape of the rostrum is not as well preserved in these as it is in the fossil from Birkenfeld. Thus the family must have survived throughout the Upper Carboniferous and the Permian, in Europe.

These insects must have fed upon the sap of plants, like the cicadas of the present day. Example:

Eugereon böckingi Dohrn., from the Lower Permian of Birkenfeld, Thuringia. Pl. 3, IV (A).

7. Order **Megasecoptera**. This Order differs from the Eupalaeodictyoptera in many details, though in general appearance it resembles the SPILAPTERIDAE. The body is slimmer and longer, the pronotum already being reduced, and smaller than the mesothorax; the cerci always very long. Mouthparts of the chewing type, with short, strong mandibles. Eyes big, and frontal ocelli present. Prothoracic wing-pads and abdominal paranotal lobes in process of disappearing. Legs short, the fore-legs often shorter than the middle and hind pairs, and modified for holding prey and conveying it to the mouth. Tarsi five-segmented, thus differing from those of the two preceding Orders, which had them three-segmented.

Wings of the two pairs alike, with a characteristic shape, narrowed

basally and broadened in the distal part. They are drawn in at the base like those of the dragonflies of the Sub-Order Zygoptera. Very often the wings were coloured with dark spots, and with a reduced venation, in which the cross-veins were few and regular.

The Megasecoptera were clearly distinct from the Eupalaeodictyoptera in their way of life as well as in their morphology. Instead of feeding on plants they had become carnivores, like the dragonflies. In contrast to the slow, heavy flight of the Eupalaeodictyoptera, the Megasecoptera flew rapidly, and caught and devoured their prey in the air.

The larvae were aquatic, and several impressions of them have been found.

There are two sub-orders, which evolved during the Carboniferous and Permian, respectively, under different climatic conditions.

Sub-Order *Eumegasecoptera*

These species were very much like the SPILAPTERIDAE, but were still more slender, and had different wings. Wing-pads were present on the prothorax, in the form of toothed or spiny crests, and the abdominal segments had paranotal lobes. The wings were always narrowed at the base, with a reduced venation, and few cross-veins; a single anal vein was long and branched.

These insects were quite big, with an average wing-span of 10–15 cm. and lived in the hot, humid equatorial forests of the Carboniferous, along with the Eupalaeodictyoptera. They disappeared at the end of the Stephanian, or the beginning of the Permian.

Seven or eight families of Eumegasecoptera are known, most of them from Commentry. Several genera have been described from England, Russia, or even from the Lower Permian of Kansas (*Elmoa*).

Family CORYDALOIDIDAE Handlirsch. Wings with a short basal stalk, veins M and Cu forking, anal very long. Very small prothoracic wing-buds, sometimes absent.

Two genera known, from the Stephanian of Commentry. Example: *Corydaloides scudderi* Brongn., from the Stephanian of Commentry. Pl. 3, IV (B).

Family CAMPYLOPTERIDAE Handlirsch. Wings with a long stalk, and a more elaborate venation.

One species: *Campyloptera eatoni* Brongn., from the Stephanian of Commentry.

Family BRODIIIDAE Handlirsch. Wings with a long stalk, but with a very simple venation, and few cross-veins; three brown bands crossed the wings.

PLATE 3 – IV. PROTOHEMIPTERA AND MEGASECOPTERA

A. **Eugereon böckingi** DOHRN. (Eugereonidae), two-thirds natural size, from the Lower Permian of Birkenfeld, Thüringia.

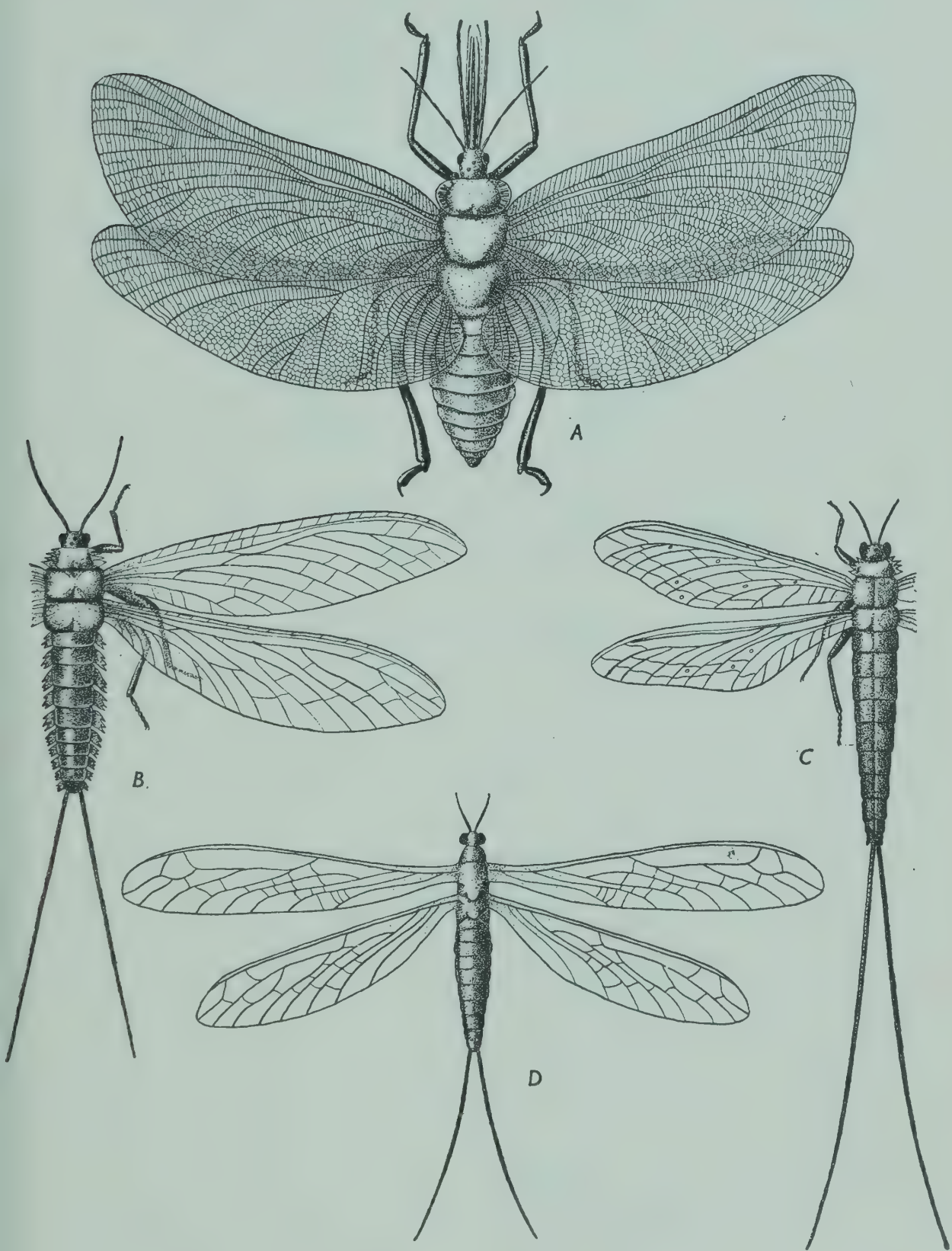
B. **Corydaloides scudderi** BRONGN. (Corydaloididae), natural size, from the Upper Carboniferous of Commentry, Allier.

C. **Mischoptera woodwardi** BRONGN. (Mischopteridae), one-half natural size, from the Upper Carboniferous of Commentry, Allier.

D. **Pseudohymen angustipennis** MART. (Protohymenoptera), twice natural size, from the Upper Permian of Posadski Log, Russia.

(Figs. A–C after reconstructions by HANDLIRSCH; fig. D after MARTYNOV.)

PLATE 3-IV. PROTOHEMIPTERA AND MEGASECOPTERA



A single genus with four species, from the Stephanian in England.
Example:

Brodia priscotincta Scudder, from the Stephanian, England (Fig. 129).

Family MISCHOPTERIDAE Handlirsch. Wings with a long stalk, triangular, with coloured spots. Venation simplified, with veins R, M and Cu arising as forks. Eyes prominent. Prothoracic wing-pads small and toothed. Cerci excessively long.

A dozen species, in five genera, all from Commeny. Example:

Mischoptera woodwardi Brongn., from the Stephanian of Commeny. Pl. 3, IV (C).

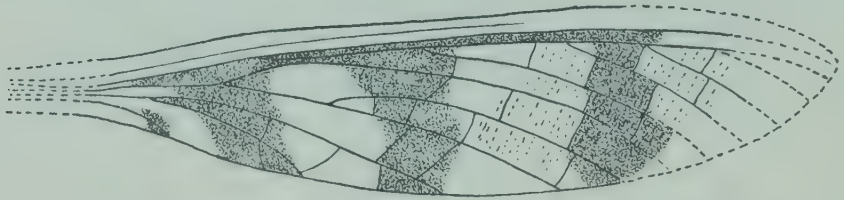


Fig. 129 – Fore-wing of *Brodia priscotincta* SCUDDER, a Eumegasecopteron from the Upper Carboniferous of England (after HANDLIRSCH).

Sub-Order *Protohymenoptera*

The first specimens of this group to be found, in the Lower Permian of Kansas, were at first taken to be the ancestors of the Hymenoptera, because of certain peculiarities in the wing-venation. In reality they are a special development of the Megasecoptera. Unfortunately, the Law of Priority obliges us to go on calling them by this name, just as we have the Protohemiptera discussed above.

Compared with the Eumegasecoptera, the Protohymenoptera are much reduced in size, and are slender and delicate in shape. The eyes are very big, and the prothorax is long and pyramidal, without wing-pads. There are no abdominal paranotal lobes, and the cerci are very long. The wings are long and stalked, with simple venation and few cross-veins; the anal vein is long, without branches.

Like the Eumegasecoptera, these insects were carnivores, and flew rapidly. They were not known in Carboniferous times, but make their first appearance in the Lower Permian of Kansas. Later they are found in the Upper Permian in Russia (Kazan and Archangel), that is to say, at the opposite edge of Laurentia.

It is not certain that these are descendants of the Eumegasecoptera, which disappeared at the end of the Carboniferous. At that time the increasing dryness of the climate of Laurentia brought about the disappearance of the great hot and humid forests, which were replaced by

temperate and even arid conditions. Here and there were marshy areas, scattered among a sparse vegetation, and here appeared a Permian fauna, which had arrived from somewhere else, and taken the place of the fauna of the Carboniferous. While the Eumegasecoptera became extinct, or migrated to other hot and humid regions, there suddenly appeared in Laurentia the Protohymenoptera, whose ancestors had evolved during the Carboniferous in some other area.

Several families of Protohymenoptera have been described, two of which, PROTOHYMENIDAE and ASTHENOHYMENIDAE were discovered first in the Lower Permian of Kansas, and then rediscovered in the Upper Permian of Russia, with five or six other new families. Example:

Pseudohymen angustipennis Mart., from the Upper Permian of Posadskij. Pl. 3, IV (D).

Incertae Sedis

Sypharopteroidea. Handlirsch erected this Order for a small species from the Middle Carboniferous of Mazon Creek, Illinois, which he named *Sypharoptera pneuma*. The fossil imprint shows that the wings were alike, and folded backwards, in this respect resembling the wings of the Neoptera. Martynov is of the opinion that this attitude of the wings may be fortuitous.

The wing-venation of *Sypharoptera* strongly resembles that of the SPILAPTERIDAE, and it seems fairly certain that it should be placed in that family.

Sypharoptera pneuma Handl. is illustrated in Pl. 3, III (G).

Archodonata. Martynov erected this Order for his *Permothemis libelluloides*, which he described from an impression of a wing in the Upper Permian of Iva Gora, in Archangel Province. The shape of this wing recalls the ASTHENOHYMENIDAE, but in some respects the venation is related to the Palaeodictyoptera and the Odonata. In particular, a pterostigma is present. More material must be found before *Permothemis* can be given its true systematic position.

Protodonata. Founded by Brongniart for the two genera *Protagrion* and *Meganeura*. Martynov has taken out *Meganeura*, and made it the type of his Order Meganisoptera, which will be discussed later on. With *Protagrion* he has linked the genera *Calvertiella* and *Tillyardiella*, from the Upper Permian of Russia, and *Permagrion* from the Stephanian of Commeny.

All these genera are based merely upon imprints of wings. When they are better known we shall no doubt find that they have no connexion with the Odonatoptera, since there is every reason to believe that we are really dealing with primitive Megasecoptera.

Hadentomoidea. Handlirsch proposed this Order for a number of

fossil imprints from the Carboniferous, which he thought were Palaeodictyoptera with a wing-venation leading on to that of the Embioptera. The true systematic position of these insects has yet to be determined. Example:

Hadentomum americanum Handl., of the Middle Carboniferous of Mazon Creek, Illinois. Pl. 3, III (H).

Superorder EPHEMEROPTEROIDEA

The main distinguishing mark of these Palaeoptera is the presence of an unpaired paracercus between the two cerci on the eleventh abdominal segment. Two Orders are included, *Protephemeroptera* and *Plectoptera* (or *Ephemeroptera*).

8. Order **Protephemeroptera**. These insects were dominant during the Carboniferous. They were fairly big and had two pairs of similar wings, which they held out flat when at rest, like the Palaeodictyoptera. The mouth was orthognathous, and of a chewing type; the antennae were slender, and there were three frontal ocelli. There were neither prothoracic wing-pads, nor paranotal lobes of the abdominal segments, but the segments of the thorax were alike, and so were those of the abdomen.

The wings were all four alike, oblong, with a rounded tip. The venation is very similar to that of living *Ephemeroptera*, including intercalary veins.

With their similar wings, held flat when at rest, these *Protephemeroptera* cannot be taken as ancestral to the true *Ephemeroptera*. The fact that they are present in the Carboniferous shows that the *Ephemeropteran* stock branched out early in the Palaeozoic, and that one branch of it, the *Protephemeroptera*, specialized during the Carboniferous and then became extinct, along with the *Eupalaeodictyoptera* and the *Eumegasceoptera*, when the hot and humid forests vanished from Laurentia.

This Order is based upon a single family.

Family *TRIPLOSOBIDAE* Handlirsch. One single known species, with a wing-span of 4.5 cm., namely:

Triplosoba pulchella Handl., from the Stephanian of Commeny. Pl. 3, VI (A).

9. Order **Plectoptera**. The *Plectoptera*, or *Ephemeroptera*, are one of the most important groups of aquatic insects at the present day, but their history goes back to the Palaeozoic. Without being conclusively proved, it seems likely that they arose in Gondwanaland after the end of the Carboniferous. It is a fact that they replaced the *Protephemeroptera* as soon as Laurentia became arid, and appeared in a succession of migratory waves. The first of these, in the Permian, gave rise to the *Permoplectoptera*, and the later migrations, in Mesozoic times, gave us the living *Ephemeroptera*.

All these *Plectoptera*, however, retained the archaic structure of the

Protephemeroptera. Even in the living species the abdominal segments remain homonomous, and all the organs have kept their primitive structure. The mouthparts, the thorax and the wings, on the other hand, have become more specialized by small steps, which can be followed in sequence in the fossil record.

Sub-Order *Permoplectoptera*

These primitive Ephemeroptera still had their two pairs of similar wings, and still had not started upon the progressive reduction of the hind-wings which comes near to abolishing them altogether in the living *Cloeon*. The mouthparts were still well developed.

This group makes its appearance in the Lower Permian deposits of Elmo, Kansas, and the fossils, which are particularly well preserved, are grouped into several families, notably PROTEREISMATIDAE, DOTERIDAE, and MISTHODOTIDAE. Martynov found others in the Upper Permian of Tikhie Gory and Iva Gora, in Russia, and put these into the family PALINGENIOPSIDAE.

It is impossible to look on these Permoplectoptera as being direct ancestors of our own Ephemeroptera, because their wings, especially those of the PROTEREISMATIDAE, were too specialized for us to derive those of the Ephemeroptera of the Mesozoic from them. Since they appear in turn at the two opposite sides of Permian Laurentia, first in Kansas, and later in Russia, they give the appearance of being immigrants from Gondwanaland. They disappeared completely at the end of the Palaeozoic.

The Upper Permian deposits of Orenburg have yielded very well-preserved imprints of larvae of Ephemeroptera (*Phthartus rossicus* Handl.), which must belong to the Permoplectoptera. Further, they have primitive characters, such as independent wing-buds, and nine pairs of abdominal tracheal gills. Pl. 3, VI (B).

Sub-Order *Euplectoptera*

Very little is known about the Ephemeroptera of the Mesozoic period. Two families, PAEDEPHEMERIDAE and MESEPHEMERIDAE have been erected for imprints of wings from the lithographic deposits of the Upper Jurassic of Solenhofen. These show that there was already a tendency for the hind-wings to become reduced in size, but very primitive features in the wing-venation prove that we are dealing with new stocks, no doubt migrated from Gondwanaland, like the Permoplectoptera, but succeeding the latter in time. Larval imprints are known from Siberia. Pl. 3, VI (C).

As for the modern families of Ephemeroptera, these are scarcely known before the Oligocene. Representatives of living genera have been

found as fossils here and there throughout the Tertiary deposits of various parts of the world.

Superorder ODONATOPTERA

This group comprises two Orders, the *Meganisoptera* and the Odonata proper, of which the second are known from a great many fossil imprints from Carboniferous times. As with the Ephemeroptera, there were two independent lines, the first of which came to a premature end, while the second was a newcomer in Mesozoic times.

10. Order **Meganisoptera**. These archaic dragonflies were dominant in the Carboniferous, in the hot and humid forests of Laurentia, at the same time as the Eupalaeodictyoptera, but their stock was able to survive throughout the Permian and the Mesozoic, adapting itself to the increasing aridity. They became extinct only in the Jurassic.

In general shape these Meganisoptera were very much like Aeschnidae, but right from the start they were of a gigantic size. *Meganeura monyi* had a wing-span of 70 cm., and a splendid specimen can be seen in the Gallery of Palaeontology at the *Muséum National d'Histoire Naturelle*, Paris. Their characters were a mixture of primitive structures and advanced specializations. The pronotum had suffered scarcely any reduction, and the abdominal segments were relatively broad, and more or less homonomous. The head, however, already showed characters of the dragonflies, while all trace of prothoracic wing-pads and of abdominal paranotal lobes had vanished. The wings were shaped like those of the Aeschnidae, broad at the base, and held out flat when at rest, but they had no pterostigma, no nodus, and no arculus, at least among the Carboniferous species. The venation was very abundant, and highly evolved compared with that of the Palaeodictyoptera.

Family MEGANEURIDAE Martynov. This family is represented in the European Carboniferous by several species, some of them of giant size. Example:

Meganeura monyi Brongn., from the Stephanian of Commentry. Pl. 3, V.

In the Permian species of the same family, but of a smaller size, make up the sub-family TYPINAE. The genus *Typus* was described from the Lower Permian of Kansas, the genera *Arctotypus* and *Megatypus* from the Upper Permian of the provinces of Kazan and Kargala in Russia.

MEGANEURIDAE appear again in the Lias of Turkestan, and form the sub-family LIADOTYPINAE, of still smaller size. The latest known fossils date from the Jurassic.

Thus the Meganisoptera can be seen as a line of dragonflies that came into being in Laurentia in Carboniferous times, and gave rise to giant

forms in the hot and humid forests of that period. While they were able to withstand the climatic changes of Permian times, the descendants of these Carboniferous giants reduced their size bit by bit, and so were able to survive right up to the Jurassic. In the end they became extinct, leaving no descendants, and were replaced by the true Odonata, which arose in Gondwanaland and spread widely throughout the entire world in the Mesozoic.

11. Order **Odonata**. Although the evolution of this Order is an involved story it can be reconstructed because fossil imprints of wings, and even of entire insects, are very numerous. The oldest of them date from the Permian, and they have been recorded from nearly all the fossil-bearing strata of the Mesozoic and of the Tertiary.

Living Odonata fall into three Sub-Orders, the great majority of them falling into the first two of these. Thus:

Anisoptera (*Aeschna*, *Libellula*, *Gomphus*), with wings broad at the base, with a rich venation, and held out flat when at rest.

Zygoptera (*Agrion*, *Calopteryx*), which hold the wings up and press them back to back when at rest, and have the wings stalked at the base, and with a reduced venation.

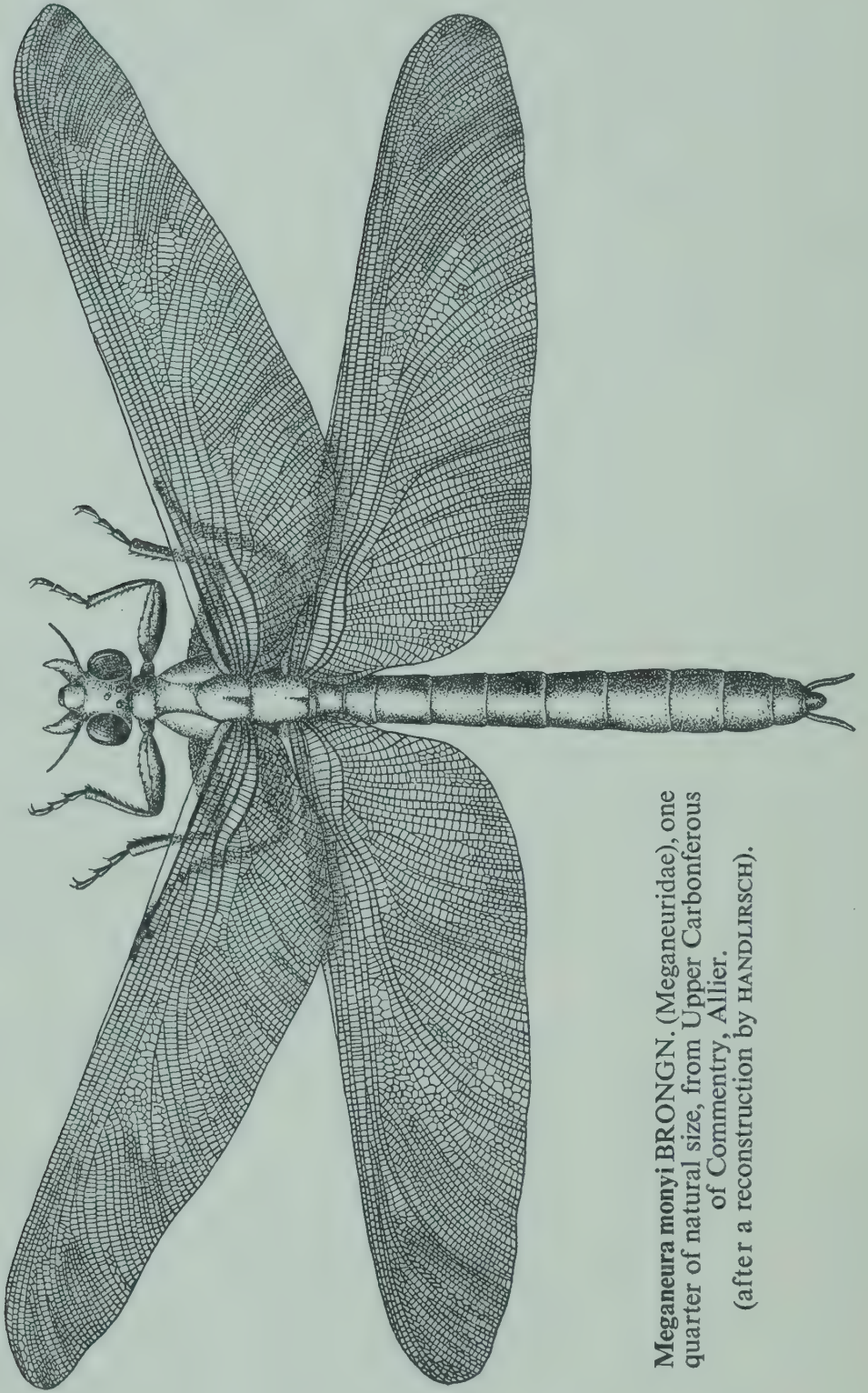
Finally, *Anisozygoptera*, in which the discal cell is open in the fore-wing, though closed in the hind-wing. There are only two living species of this group, one in Japan and one in Asia.

The imprints of wings in the fossil record show these three groups, right down from Permian times, and it was believed at one time that the three groups of living Odonata could be derived directly from the Permian forms. Martynov has correctly pointed out that the Permian forms have certain details in which they are more highly evolved than the Cretaceous and Tertiary dragonflies, so that it is not reasonable to consider them to be ancestral to these.

We cannot go in detail into the various theories of Handlirsch, Tillyard and Carpenter on the affinities of the Odonata, and there is space only to say that opinion supports Martynov's view that the Odonata of the Permian cannot have been direct ancestors of those of the Mesozoic and Tertiary. The former (Permian Odonata) seem to have been a sort of 'Permian edition' of the various evolutionary possibilities of the stock, which were then repeated during the Mesozoic and Tertiary among the various stocks that migrated from Gondwanaland (Neodonata).

It can be supposed, therefore, that the primitive stem of all the Odonata arose in Gondwanaland during the Palaeozoic, and continued to flourish there throughout the Mesozoic. Migrations northward followed each other in successive geological periods, giving rise first to the Permian Odonata, then later on to the Neodonata. These followed each other in relays, occupying the same continents and producing there similar evolutionary

PLATE 3-V. MEGANISOPTERA



Meganeura monyi BRONGN. (Meganeuridae), one quarter of natural size, from Upper Carboniferous of Commeny, Allier.
(after a reconstruction by HANDLIRSCH).

types. As Martynov said, the relationship between the two groups is the same as that between Marsupials and Placentals.

Group PERMODONATA

This group brings together a number of extinct Sub-Orders, of which the principal ones are *Protozygoptera*, *Archizygoptera*, *Protanisoptera* and *Permanisoptera*. Members of these Sub-Orders first appear in the Lower Permian deposits of Kansas, then in the Upper Permian in Russia. Traces of them can be found in Permo-Triassic beds in Australia and the Falkland Islands, thus supporting the theory that these groups arose as migrants from Gondwanaland.

Sub-Order *Protanisoptera*

Fossil imprints of wings that fall into this Sub-Order are found in the Lower Permian of Kansas (*Ditaxineura* Tillyard, *Camptotaxineura* Tillyard); from the Upper Permian of Belmont, in Australia (*Polytaxineura* Tillyard) and from Tikhie Gory, in the Province of Kazan, Russia (*Pholidoptilon* Zal.).

These Permian dragonflies foreshadow the Anisozygoptera, which were to flourish in the Mesozoic.

Sub-Order *Permanisoptera*

Erected for the genus *Permaeschna* Martynov, from the Upper Permian of Iva Gora, in Archangel Province. They have some of the characters of the Anisoptera, which were represented in Mesozoic Europe by a number of GOMPHIDAE.

Sub-Order *Protozygoptera*

An abundant group, which during the Permian radiated vigorously along all the lines that were later followed by the Zygoptera, thus:

The KENNEDYIDAE, with three genera, *Kennedya*, *Opter* and *Progoneura* from the Lower Permian of Kansas, had characters which anticipated the AGRIONIDAE.

The PERMOLESTIDAE, from the Upper Permian of Archangel, and the PERMOPALLAGIDAE from the same levels of the River Sojana, foreshadow the LESTIDAE and AGRIONIDAE.

The TRIASSOLESTIDAE, from the Upper Trias of Ipswich, in Australia have analogous characters, but the Australian Protozygoptera have also more primitive characters, such as the persistence of numerous prenodal veins, which underline the fact that these are survivors of the primitive Gondwanian stock, from which the other families have arisen.

PLATE 3 – VI. PROTEPHEMEROPTERA,
PLECTOPTERA & ODONATA

A. **Triplosoba pulchella** HANDL. (Triplosobidae), twice natural size, from the Upper Carboniferous of Commentry, Allier.

B. **Larva of Phthartus rossicus** HANDL. (Permoplectoptera), natural size, from the Upper Permian of Orenburg, Russia.

C. **Larva of Mesoleucta gracilis** BRAUER (Euplectoptera), twice natural size, from the Middle Jurassic of Siberia.

D. **Tarsophlebia eximia** HAGEN (Anisozygoptera), one-and-a-half times natural size, from the Upper Jurassic of Bavaria.

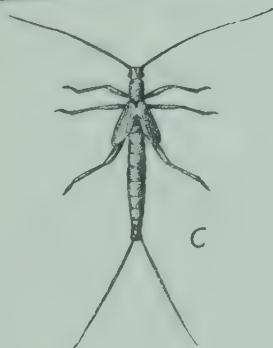
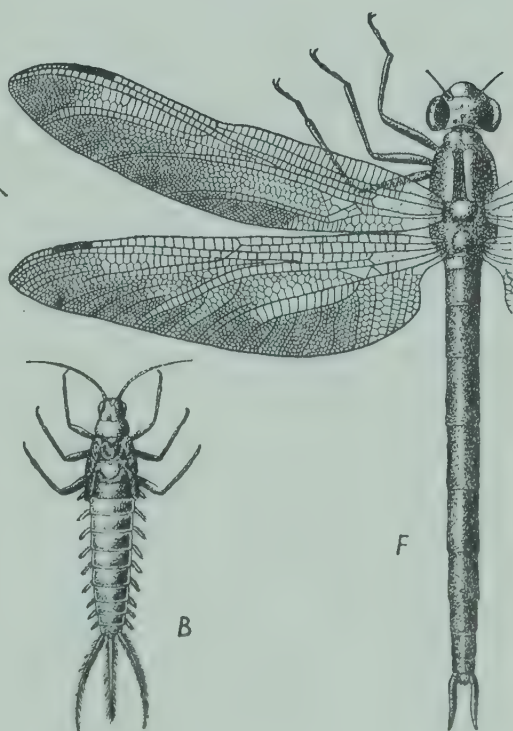
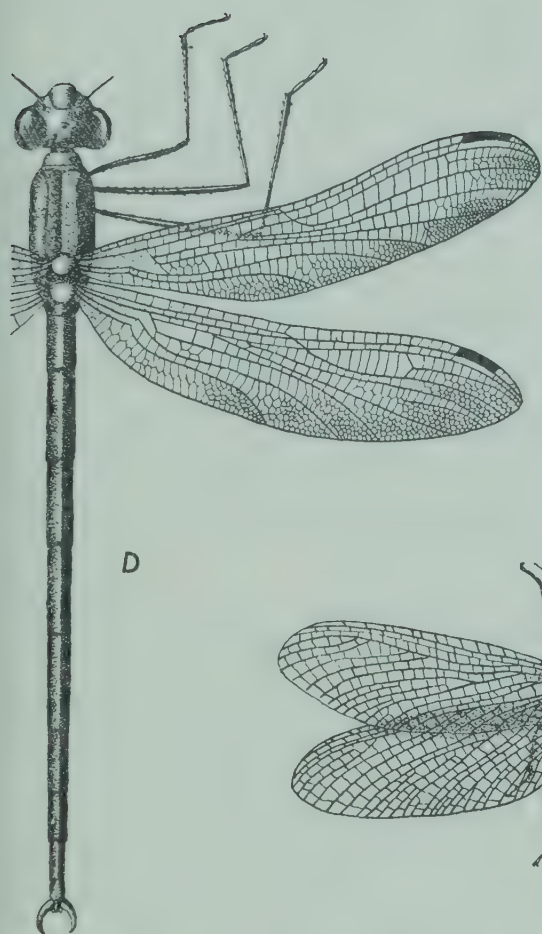
E. **Stenophlebia latreillei** GERM. (Anisozygoptera), natural size, from the Upper Jurassic of Bavaria.

F. **Prolindenia wittei** GIEB. (Anisozygoptera), natural size, from the Upper Jurassic of Bavaria.

G. **Aeschnidium densum** HAGEN. (Anisoptera), natural size from the Upper Jurassic of Bavaria.

(After reconstructions by HANDLIRSCH)

PLATE 3-VI. PROTEPHEMEROPTERA,
PLECTOPTERA & ODONATA



Sub-Order *Archizygoptera*

This is an aberrant group, placed near the Protozygoptera. It includes *Triassagrion* Till., from Ipswich, and the genera *Protomyrmeleon* Handl. and *Tillyardagrion* Mart. from the European Lias.

GROUP NEODONATA

We have just seen how several diverse lines of Permodonata seem to have arisen from Gondwanian stems, and have reached various points in Laurentia, Kansas, Russia and Europe, by successive migrations. After having lasted some 80 million years, these Permodonata became extinct, but other lines no doubt originating from the same Gondwanian stems, have followed after them. These make up the group of Neodonata, which still survive today.

Since they had the same origin, and followed the same migratory routes into the Northern Hemisphere, it is not surprising that these Neodonata should show some of the same orthogenetic trends in their evolution.

The evolutionary lines in the Neodonata are fewer and less diverse than those in the Permodonata. They fall into three groups, one of which is on the point of extinction at the present time.

Sub-Order *Anisozygoptera*

These are the kind of dragonflies that occupied the world stage during the Mesozoic. There were a number of families, ARCHITHEMIDAE, TARSOPHLEBIIDAE, STENOPHLEBIIDAE, ISOPHLEBIIDAE, etc., all of which are now extinct. Their imprints are to be found in the Lias of Mecklenburg, and of England, as well as in the Upper Jurassic, and particularly in the lithographic deposits of Solenhofen, in Bavaria.

After a great blossoming out in the Jurassic, all these Anisozygoptera disappeared in the Cretaceous. Only one genus, *Epiophlebia* (family EPIOPHLEBIIDAE), with one species in Japan and one in Asia, persists today as a relict. Examples:

Tarsophlebia exima Hagen, from the Upper Jurassic of Bavaria. Pl. 3, VI (D).

Stenophlebia latreillei Germ., from the Upper Jurassic of Bavaria. Pl. 3, VI (E).

Prolindenia wittei Gieb., from the Upper Jurassic of Bavaria. Pl. 3, VI (F).

Sub-Order *Zygoptera*

The first dragonflies of this Sub-Order appeared in the Upper Lias of Mecklenburg (EOSAGRIONIDAE), then came the EPALLAGIDAE in the Upper Jurassic of Bavaria.

In the Tertiary are found fossil imprints of wings of CAENAGRIONIDAE, and the remains of true LESTIDAE and AGRIONIDAE, that is to say, species belonging to families that still persist to the present day.

Sub-Order *Anisoptera*

These replaced the Permanisoptera, and must be linked with *Aeschniopsis* from the Upper Trias of Ipswich, in Australia, which shows once again the Gondwanian origin of the Sub-Order.

In Europe, the Jurassic deposits have yielded many GOMPHIDAE, which have all the characters of living species. During the Tertiary AESCHNIDAE, GOMPHIDAE and LIBELLULIDAE appeared in numbers. Example from the Jurassic:

Aeschnidium densum Hagen, from the Upper Jurassic of Bavaria. Pl. 3, VI (G).

B. SECTION POLYNEOPTERA

Superorder BLATTEROPTEROIDEA

Four Orders are brought together in this group: Dictyoptera, Protoblattoptera, Isoptera and Zoraptera. The first of these, which includes the Cockroaches, makes up the bulk of the insect fauna of the Palaeozoic, as it appears in the fossil record.

14. Order **Dictyoptera**. This Order brings together the Blattidae and Mantidae.

The BLATTIDAE (cockroaches) are perhaps the most ancient of all the Pterygota. It is not impossible that the imprint of a pair of mandibles found in the Old Red Sandstone (Middle Devonian) of Rhynie, in Scotland may be that of a cockroach. In any event, cockroaches that are already very specialized appear in great numbers in the earliest known deposits of the Carboniferous Period, and there are no fundamental differences between these Palaeozoic cockroaches and those of the present day. It would seem that they have survived unchanged, perhaps from Devonian times; that is to say, for about 400 million years.

Like the living cockroaches, those of the Carboniferous had a broad prothorax, flattened out, and concealing the head; fore-wings specialized as tegmina; and hind-wings broadened posteriorly by the formation of an anal fan, or *neala*. In size they must have been about the same as the living species. These Palaeozoic cockroaches lived hidden in vegetable debris, as do the living species, and no doubt this fact ensured that they were easily fossilized. They were omnivorous, and laid their eggs in egg-pods (*ootheca*).

Their nymphs differed from those of the present day in having longer wing-pads, and much longer cerci. Pl. 3, VII (A). Martynov, who noticed

the last detail, and who says that some of them had the cerci broad and flat like those of the PERLIDAE, deduces from this that the early stages of Palaeozoic cockroaches were probably aquatic.

The Palaeozoic Cockroaches

The ancestral cockroaches were probably dominant in Laurentia before the Carboniferous, and under the influence of the equatorial climate, hot and humid, that prevailed in this part of the world in the Middle and Upper Carboniferous, they became exceedingly numerous and diverse. The Order then entered into a period of expansion and variation, as other evolutionary lines have done at various geological periods. The Carboniferous Period in Laurentia was the heyday of the Palaeodictyoptera and of the cockroaches. Fossil traces are to be found in all the suitable strata of the Carboniferous, and represent more than a dozen families. Here we can only mention the principal ones:

Family ARCHIMYLACRIDAE Handlirsch. In this family we know no fewer than 360 species, arranged in 75 genera (1925), including the most ancient representatives of the Order. These cockroaches have a primitive wing-venation, recalling that of the Palaeodictyoptera.

Remains of ARCHIMYLACRIDAE have been found in nearly all the coal-measures, Westphalian or Stephanian, in Europe and North America. They are still present, though less numerous, in the Lower Permian of Kansas, the Upper Permian of Russia, and the Upper Permian of India, so that it seems as if they must have been able to adapt themselves to the more arid conditions that came into being at the end of the Palaeozoic, and to migrate towards Gondwanaland. Examples:

Aphthoroblattina johnsoni Woodw., from the Upper Carboniferous of England. Pl. 3, VII (B).

Phylloblatta carbonaria Germ., from the Upper Carboniferous of Germany. Pl. 3, VII (C).

Family SPILOBLATTINIDAE Handlirsch. This family differs from the preceding one by the evolution of the wing-veins, especially by the shortening of Sc, and basal fusions between R and M. More than 100 species of this family are known, in 8 genera, here and there in the Middle and Upper Carboniferous of North America and of Europe, and in the Permian of Central Europe. Example:

Syscioblatta dohrni Scudd., from the Upper Carboniferous of Germany. Pl. 3, VII (D).

Family MYLACRIDAE Scudder. The species of this family are all short and very broad, the thorax in particular being strongly transverse, but the definitive characters are still in the wing-venation.

These cockroaches seem to have been specially characteristic of North America, where more than 60 species, in 20 genera, have been found in various strata of the Upper Carboniferous. A few groups reached England and Northern France, and a larva is illustrated in Pl. 3, VII (F). Example:

Paramylacris rotunda Scudder., from the Middle Carboniferous of Mazon Creek, Illinois. Pl. 3, VII (E).

Family DICTYOMYLACRIDAE Handlirsch. Allied to the MYLACRIDAE, but with a venation characterized by the existence of very many cross-veins, amounting almost to an archedictyon. The prothorax is very broad, transverse, and sculptured into radiating ribs.

There is one genus, with two species in the Upper Carboniferous of France, and one other in the corresponding strata in Kansas. Example:

Dictomylacris poirault Brongn., from the Stephanian of Commentry. Pl. 3, VII (G).

The Cockroaches of the Mesozoic

All the preceding families disappeared at the end of the Palaeozoic, for the greater part even at the end of the Carboniferous, when the hot and humid climate began gradually to dry up. At the same time other families, which had been in existence during the Carboniferous, no doubt in places where the local climate was relatively arid, were able to withstand the climatic change, and to prevail throughout the Mesozoic, though they were much less numerous than their predecessors.

Family MESOBLATTINIDAE Handlirsch. Species that were small in size, and had a highly evolved wing-venation, especially in the costal field. About ten species are known, in five genera, from the Upper Carboniferous of Europe and America, as well as from the Lower Permian. During the Mesozoic the family flourished, so that thirty genera, with a hundred species, are known from the Trias of Tonkin, the European Lias, and even from the Upper Cretaceous in North America.

Family POROBLATTINIDAE Handlirsch. Close to the preceding family, but distinguished by certain details of wing-venation. They still remain small insects. More than thirty species are known, in four genera, the majority from the Upper Carboniferous and the Permian of North America and Central Europe. One species has been found in the Trias of Tonkin, and another from the Middle Jurassic of Siberia.

Thus we see how the Mesozoic cockroaches arose from Laurentian stems at the end of the Palaeozoic, and spread throughout the world during the Mesozoic.

PLATE 3 – VII. DICTYOPTERA

A. Larva of an *Archimylacrid*, enlarged by one-quarter, from the Upper Carboniferous in England.

B. *Aphthoroblattina johnsoni* WOODW. (*Archimylacridae*), natural size, from the Upper Carboniferous in England.

C. *Phylloblatta carbonaria* GERM. (*Archimylacridae*), enlarged by one-half, from the Upper Carboniferous in Germany.

D. *Syscioblatta dohrni* SCUDDER (*Spiloblattidae*), enlarged two-and-one-half times, from the Upper Carboniferous of Germany.

E. *Paramylacris rotunda* SCUDDER (*Mylacridae*), natural size, from the Middle Carboniferous of Mazon Creek, Illinois.

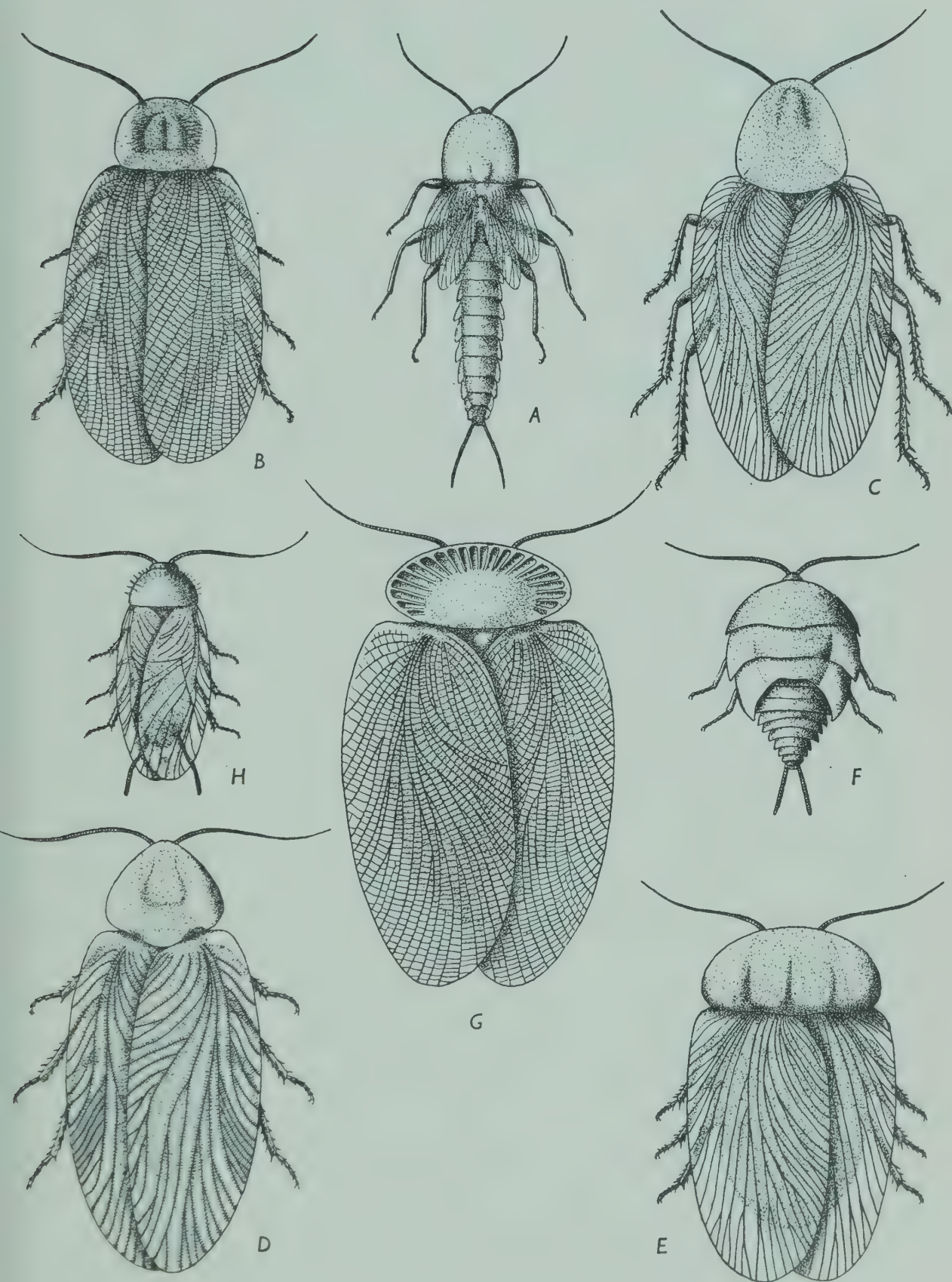
F. A larval *Mylacrid*, natural size, from the Middle Carboniferous of Mazon Creek, Illinois.

G. *Dictyomylacris poiraulti* BRONGN. (*Dictyomylacridae*), enlarged three times, from the Upper Carboniferous of Commentry, Allier.

H. *Holocompsa fossilis* SHELF. (*Corydiidae*), enlarged three times, from the Baltic Amber (Lower Oligocene).

(After reconstructions by HANDLIRSCH)

PLATE 3-VII. DICTYOPTERA



The Tertiary Cockroaches

These are now true cockroaches, little different from the living species, which are to be found sparsely throughout the Tertiary deposits. About one hundred and thirty species have been identified in the Baltic Amber (Lower Oligocene). These are insects of a warm climate, many of them belonging to groups which today are confined to the tropical fauna.

The following species belongs to the family CORYDIIDAE:

Holocompsa fossilis Shelf., from the Baltic Amber. Pl. 3, VII (H).

The Mantids

The Mantids certainly come from the same stems as the cockroaches; at first glance they seem to have little in common, but they do in fact have several points of resemblance, notably the habit of laying their eggs in egg-pods. Yet the geological history of the Mantids is hardly known.

Certainly we shall have to exclude some of the Palaeozoic groups that some authors have included in the ancestry of the Mantids, and the Palaeomantids of the Upper Permian of Russia have nothing to do with them. The most ancient fossils that we can accept as authentic Mantids go back no further than the Oligocene of the Baltic Amber.

Perhaps the lack of geological evidence about the origin of the Mantids may be explained if they were dominant in Gondwanaland, where fossil-bearing strata of the older Periods are rare.

13. Order **Protoblattoptera**. This Order consists entirely of fossil insects from the end of the Palaeozoic. They have been considered to be ancestral to the cockroaches, but nowadays it is realized that they form a big line of evolution of their own, very different from that of the cockroaches, and specialized in different directions.

The Protoblattoptera are somewhat like cockroaches, but are more elongate in shape, with the head free, not concealed by the prothorax; the latter is often very long, with a long stalk. The mouth was orthognathous, and of a chewing type. The tarsi were five-segmented. Finally, the wings were always very elongate, folded backwards when at rest, and quite different from those of cockroaches. The fore-wings were not specialized as tegmina, and took part in flight. Vein R branched into two, R and R_s, and the branches of R_s supported the distal area of the wing, with positive and negative veins forming ridges like those of the Orthopteroidea.

In spite of their apparent resemblance to cockroaches the Protoblattoptera had very different habits. They were quite big (3–6 cm. long), and flew easily about the herbage, probably catching living prey. Several immature forms are known, notably one very well-preserved specimen from the Upper Permian of Koungour, in Russia. This is like a nymphal cockroach, but with much longer cerci. Martynov, who discovered it,

says it was aquatic, because he considers that delicate, leaf-like cerci are always a clue to an aquatic habitat.

The fact that Protoblattoptera cannot be ancestral to the cockroaches, as Handlirsch thought them to be, is confirmed by their later appearance on the scene. The oldest of them dates from the Upper Westphalian, but then they evolved with great rapidity, so that we can speak of them as having 'arrived' by Stephanian times (Commentry), when they were both abundant and diverse.

Protoblattoptera continued during the Permian, but disappeared completely before the end of the Palaeozoic. So they were a comparatively short-lived race, lasting for no more than 50 million years.

Among the main families we may mention the following:

Family PROTOPHASMIDAE Brongniart. This family was erected for a species that is remarkable in possessing a true archedictyon in the wing, and which was at first erroneously thought to be ancestral to the PHASMIDAE. Examples:

Protophasma dumasi Brongn., from the Stephanian of Commentry. Pl. 3, VIII (A). With this must be united the EOBLATTIDAE of Handlirsch, which shares the same characters.

Eoblatta robusta Brongn., from the Stephanian of Commentry. Pl. 3, VIII (B). With these must be merged the STENONEURIDAE, of which the typical species differs from the others only in having a narrower prothorax.

Stenoneura fayoli Brongn., from the Stephanian of Commentry. Pl. 3, VIII (C).

Family ASYNCRITIDAE Handlirsch. Body very long, prothorax elongate and conical; wings very long, with the veins forming broad polygonal cells. Examples:

Asyncritus reticulatus Handlirsch, from the Carboniferous of Mazon Creek, Illinois. Pl. 3, VIII (D).

Epideigma elegans Handl., from the Carboniferous of Mazon Creek, Illinois. Pl. 3, VIII (E).

Family ADIPHLEBIIDAE Handlirsch. Characterized by the great development of the prothorax. The cross-veins of the wing are more highly evolved than the preceding, and the polygonal cells have gone; costal veins much shortened. Example:

Adiphebia lacoana Scudd., from the Middle Carboniferous of Mazon Creek, Illinois. Pl. 3, VIII (F).

Family EUCAENIDAE Handlirsch. Fore-wings more heavily chitinized, and more closely approaching the tegmina of the cockroaches. Wing-venation simplified, without cross-veins. The fore-femora had a groove on

PLATE 3 – VIII. PROTOBLATTOPTERA

A. **Protophasma dumasi** BRONGN. (Protophasmidae), one-half natural size, from the Upper Carboniferous of Commentry, Allier.

B. **Eoblatta robusta** BRONGN. (Eoblattidae), one-half natural size, from the Upper Carboniferous of Commentry, Allier.

C. **Stenoneura fayoli** BRONGN. (Stenoneuridae), natural size, from the Upper Carboniferous of Commentry, Allier.

D. **Asyncritus reticulatus** HANDL. (Asyncritidae), enlarged by half from the Middle Carboniferous of Mazon Creek, Illinois.

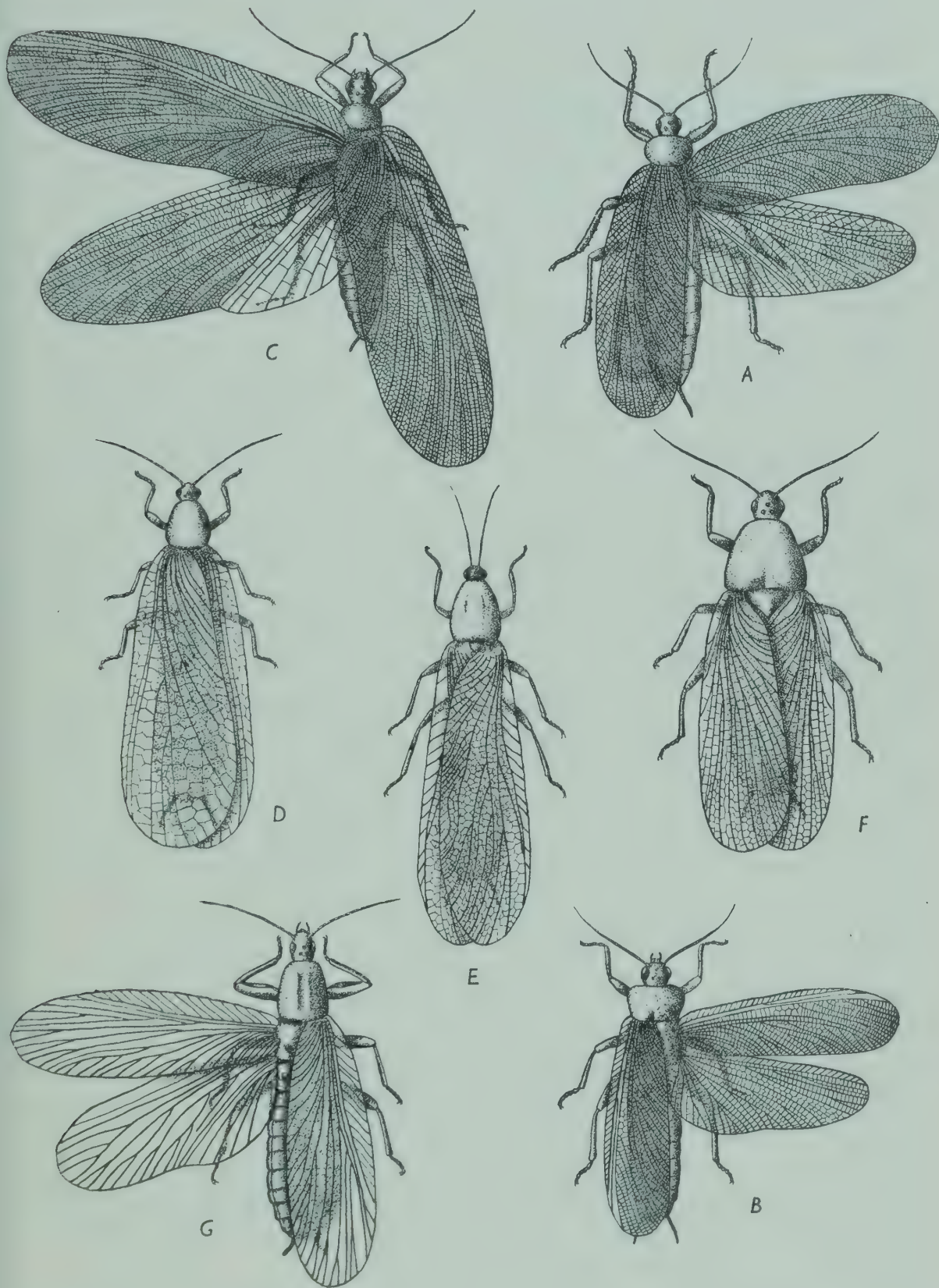
E. **Epideigma elegans** HANDL. (Asyncritidae), enlarged by half, from the Middle Carboniferous of Mazon Creek, Illinois.

F. **Adiphebia lacoana** SCUDDER (Adiphebiidae), natural size, from the Middle Carboniferous of Mazon Creek, Illinois.

G. **Eucaenus ovalis** SCUDDER (Eucaenidae), twice natural size, from the Middle Carboniferous of Mazon Creek, Illinois.

(After reconstruction by HANDLIRSCH)

PLATE 3-VIII. PROTOBLATTOPTERA



the anterior face, into which the fore-tibiae could be folded back. These are the most highly evolved of the Protoblattoptera. Example:

Eucaenus ovalis Scudd., from the Middle Carboniferous of Mazon Creek, Illinois. Pl. 3, VIII (G).

14. Order **Isoptera**. Holmgren derived the termites directly from the Protoblattoptera, but in Martynov's opinion, although the termites and the Protoblattoptera are certainly closely related, they have arisen from a common stem in the Devonian, to which he has given the name 'Archisoptera'.

In fact, we find in the termites the same primitive organization that was present in the Protoblattoptera, notably the cranial sutures and the structure of the thorax. Their wings, for the most part, have remained homonomous and membranous, and the venation is little evolved, except for the loss of cross-veins. Their most distinctive feature is the absence of a neala, which is characteristic of the Polyneoptera, but in the Mastotermitidae of the present day there is a small fan-like extension of the jugal field.

The existence of the ancestral Archisoptera is purely hypothetical, and if there ever was such a group it must have been at some very remote period. The termite stock must have departed from this line while the neala was still not evolved, and this stage must be put back, at least to the Devonian.

Traces of termites are actually found for the first time in the Tertiary, in the Baltic Amber (Lower Oligocene): these are TERMITIDAE and CALOTERMITIDAE. The absence of fossils in the Mesozoic leads us to believe that these insects must at that period have still been solitary, or lived in only small colonies in the earth, or in the interior of plants. Their great expansion came when they adopted a social life, which did not come about until comparatively late.

15. Order **Zoraptera**. These tiny tropical insects (*Zorotypus*) are very local and scarce in the present fauna, and are not known as fossils.

Superorder ORTHOPTEROIDEA

This immense group combines one extinct Order, Protorthoptera, with four living Orders, Plecoptera, Notoptera, Phasmoptera and Orthoptera. Their origins go back to the Palaeozoic.

In all the insects of this group except the Plecoptera there is a specialized ovipositor, formed from valves arising from the female genital armature. The eggs are laid singly, not massed into a true ootheca. The tarsi have only three or four segments.

16. Order **Protorthoptera**. The Protorthoptera of Handlirsch (1908) were a heterogeneous group, combining running and jumping types, but

clearly arranged round a central family, the SPANIODERIDAE. Martynov was right to dismember them, but it is not possible to follow him when he proposes to substitute the name 'Paraplecoptera' for that formerly given by Handlirsch.

The many families grouped together here as Protorthoptera are all cursorial species, that is to say the hind-legs are short, and adapted for running, not for jumping. These species are of the 'Perloid' type, with short head, mouth more often prognathous than orthognathous, mouth-parts of the chewing type. The prothorax is elongate, leaving the head free, and often, even, supporting it on the long, slim neck. According to Handlirsch the tarsi were three-segmented.

Fore-wings membranous, with the venation highly evolved, that is with the veins branched, but fewer than those of the Protoblattoptera. Hind-wings a little broadened in the ano-jugal region. Abdomen provided with segmented cerci, and the females with an elongate ovipositor.

The Protorthoptera were dominant during the Carboniferous and Permian, in Laurentia, and were fairly big insects (3–8 cm. long), with long wings, and therefore good fliers. No doubt they lived on the vegetation, and may have been either saprophagous or carnivorous. Their early stages are unknown.

Many families have been erected, and distributed among several Sub-Orders whose validity is doubtful. Here are the important ones.

Family SPANIODERIDAE Handlirsch. Slender species, with an elongate prothorax, short antennae, and three almost similar pairs of legs. Females with a short ovipositor. Hind-wings shorter than the fore-wings, the neala quite well developed; both pairs with many straight cross-veins.

A score of known species are placed in eleven genera, all from the Upper Carboniferous of North America. Examples:

Spaniodera ambulans Handl., from the Middle Carboniferous of Mazon Creek, Illinois. Pl. 3, IX (A).

Gyrophlebia longicollis Handl., from the Middle Carboniferous of Mazon Creek, Illinois. Pl. 3, IX (B).

Sthenarocera pachytyloides Brongn., from the Stephanian of Commentry. Pl. 3, IX (C).

Family ISCHNONEURIDAE Handlirsch. Hardly different from the foregoing, except in the much longer wings, in which the veins are much branched, and the cross-veins more numerous.

A single species, from the Upper Carboniferous of France:

Ischnoneura oustaleti Brongn., from the Stephanian of Commentry. Pl. 3, IX (D).

Family GERARIDAE Handlirsch. Remarkable for the excessively long fore part of the prothorax, which carries the head at the end of a long

PLATE 3 IX. PROTORTHOPTERA

A. **Spaniodera ambulans** HANDL. (Spanioderidae), natural size, from the Middle Carboniferous of Mazon Creek, Illinois.

B. **Gyrophlebia longicollis** HANDL. (Spanioderidae), two-thirds natural size, from the Middle Carboniferous of Mazon Creek, Illinois.

C. **Sthenarocera pachytyloides** BRONGN. (Spanioderidae), one-third natural size, from the Upper Carboniferous of Commentry, Allier.

D. **Ischnoneura oustaleti** BRONGN. (Ischnoneuridae), two-thirds natural size, from the Upper Carboniferous of Commentry, Allier.

E. **Gerarus longicollis** HANDL. (Geraridae), enlarged by one-half, from the Middle Carboniferous of Mazon Creek, Illinois.

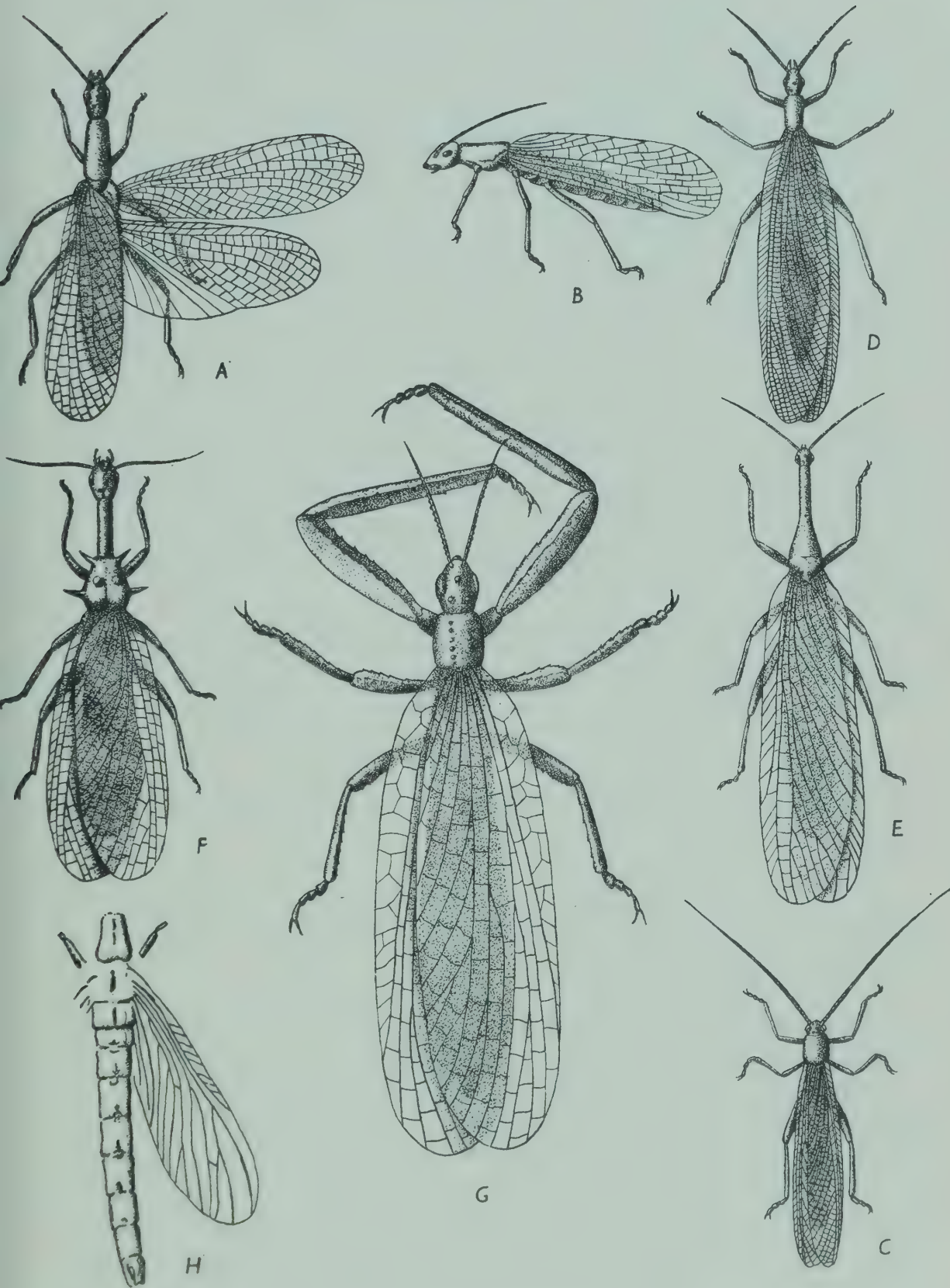
F. **Gerarus danielsi** HANDL. (Geraridae), natural size, from the Middle Carboniferous of Mazon Creek, Illinois.

G. **Cnemidolestes woodwardi** BRONGN. (Cnemidolestidae), natural size, from the Upper Carboniferous of Commentry, Allier.

H. **Apithanus jocularis** HANDL. (Apithanidae), enlarged by one-half, from the Middle Carboniferous of Mazon Creek, Illinois.

(After reconstructions by HANDLIRSCH)

PLATE 3-IX. PROTORTHOPTERA



stalk. Sometimes the posterior lobe of the prothorax bristles with spines. The other characters are much the same as in the SPANIODERIDAE.

A dozen species are known, from the Upper Carboniferous of North America. Examples:

Gerarus longicollis Handl., from the Middle Carboniferous of Mazon Creek, Illinois. Pl. 3, IX (E).

Gerarus danielsi Handl., from the Middle Carboniferous of Mazon Creek, Illinois. Pl. 3, IX (F).

Family CACURGIDAE Handlirsch. Species with the wings short and broad, vein R_s separating from R quite a long way from the base of the wing. The details of the rest of the body are poorly known. Formerly this family was raised into a separate Order, Cacurgoidea of Handlirsch, which Pruvost put along with the Protoblattoptera under the name 'Archiblattoidea'.

CACURGIDAE are known from a number of different strata of the Middle and Upper Carboniferous, mainly from North America, but also from France and Belgium. *Archimastax americanus* Handlirsch from Fayetteville, in Arkansas, comes from a level at the extreme base of the Middle Carboniferous, and is one of the oldest known fossils of the Carboniferous Period.

Family CNEMIDOLESTIDAE Handlirsch. The prothorax is short, but the fore-legs are disproportionately developed; no doubt they were prehensile, like those of the Mantids. The wings were big and the antennae short.

A single genus with two or three species, in the Upper Carboniferous of France:

Cnemidolestes woodwardi Brongn., from the Stephanian of Comentry. Pl. 3, IX (G).

Family APITHANIDAE Handlirsch. Body slender, prothorax short and pear-shaped. Fore-legs very short. Wing-venation very specialized, without cross-veins.

The systematic position of this family is still in doubt, and as far as our present knowledge goes we can only place it provisionally among the Protorthoptera. There is one species known:

Apithanus jocularis Handlirsch, from the Middle Carboniferous of Mazon Creek, Illinois. Pl. 3, IX (H).

Handlirsch has placed alongside the Protorthoptera a series of independent Orders, based upon more or less badly preserved imprints of wings from Carboniferous deposits in North America and in Europe. These are the *Mixotermioidea*, *Reculoidea* and *Haplopteroidea*. As far as one can see, none of these groups is worth keeping, and all the imprints are just imperfect remains of Protorthoptera.

Thus, as we have seen, all these Protorthoptera flourished in the equatorial fauna of Laurentia during the Carboniferous. The relative dryness of the Permian climate brought about their disappearance at the same time as that of the Eupalaeodictyoptera, whether they became extinct, or migrated somewhere else. They were replaced by the Plecoptera.

17. Order **Plecoptera**. It seems clear that the Plecoptera (commonly called 'Stoneflies', or 'Perlids') were originally Gondwanian. Like the Odonata and the Ephemeroptera, we find that they first had Permian stocks which replaced the primitive Carboniferous groups in Laurentia, and then had more recent lines the evolution of which is still in progress at the present day. The parallel between the evolution of the Plecoptera and that of the Odonata and Ephemeroptera, which is better known, suggests that the complete story may be similar, and that we should be justified in assuming that the Plecoptera, also were derived from a stem in Gondwanaland.

The Plecoptera appear in the deposits of the Northern Hemisphere in the same period as the Permodonata and the Permoplecoptera. These Permian Plecoptera, or Protoperlaria, were succeeded by other Mesozoic and Tertiary lines, called the Euplecoptera.

All these Plecoptera, Permian and recent, are characterized by the presence of a pair of multi-segmented cerci, and by the wing-structure, in which the cross-veins do not run together (haploneurous), and there is no precostal field. The head is prognathous, like that of the Protorthoptera. The early stages were always aquatic.

Sub-Order *Protoperlaria*

Tillyard erected this Sub-Order for several genera from the Lower Permian of Kansas, which had the general structure of Plecoptera, but with a very primitive organization. These Permian fossils constitute the group LEMMATOPHORIDAE, which are quite well known, thanks to the work of Sellards, and which have since been found in the Lower Permian in Europe.

Into the same Sub-Order Protoperlaria, we have to put, along with the LEMMATOPHORIDAE, a whole series of families—IDELIDAE, LIOMOPTERIDAE, PERMOCAPNIIDAE, CAMPTONEURIDAE—which Martynov had grouped under the name 'Idelodea', and placed alongside the Protorthoptera. The fossil imprints come from the Lower Permian of Kansas (LIOMOPTERIDAE), or the Upper Permian of Russia. All these groups of Protoperlaria, including the Idelodea, thus appeared suddenly in the steppelands of Permian Laurentia, first in Kansas, and then in Russia. No doubt their stem-groups must have divided off in Carboniferous times in Gondwanaland, perhaps from some group of Protorthoptera that were able to adapt themselves to a drier climate.

The Protoperlaria mostly vanished at the end of the Palaeozoic, though some few survived in the Mesozoic, at least until the Lias (*Geinitzia*). Carpenter has recorded imprints of aquatic larvae of Protoperlaria from North America.

Family LEMMATOPHORIDAE Sellards. These insects looked like stoneflies. The adult had functional mouthparts, and there were prothoracic wing-pads comparable to those of the Palaeodictyoptera, as well as paranotal lobes on the abdominal segments.

Several genera are known: one (*Lemmatophora*) from the Lower Permian of Kansas; another (*Germanoprisca*) from the Lower Permian of Germany; a third (*Kazanella*) from the Upper Permian of the Russian Province of Kazan. Example:

Lemmatophora typica Sell., from the Lower Permian of Elmo, Kansas. Pl. 3, X (A).

Family IDELIDAE Martynov. The central family of the group Idelodea of Martynov, who has repeatedly insisted in his later works upon the probable relationship between his Idelodea and the LEMMATOPHORIDAE, a relationship which seemed to him ' . . . more and more obvious as one finds that some of them possessed prothoracic wing-pads' (1938).

Family PERMOCAPNIIDAE Martynov. Martynov erected this family for species from the Upper Permian of Russia, and placed it in his Idelodea. The species have the general appearance of stoneflies, but have no prothoracic wing-pads. Example:

Permocapnia brevipes Mart., from the Upper Permian of Russia. Pl. 3, X (B).

Sub-Order Euplecoptera

True stoneflies are known as fossils from the Permian onwards. Almost all the evolutionary lines have direct descendants still alive, showing that they have managed to survive for a very long time. Everything points to the fact that they originated in Gondwanaland, and spread throughout the world by a series of migrations.

Stoneflies have been described by Tillyard from the Upper Permian of Belmont, in New South Wales. The genus *Stenoperlidium* belongs to the family EUSTENIIDAE, of which there are still living members in Australia and New Zealand. Others, that Handlirsch described from deposits in Kargala and Martynov from the Province of Archangel (*Hypoperla*), are closely related to the Australian *Stenoperlidium*, a fact which underlines the probability that they were of Gondwanian origin.

From the Lias of Western Asia and of Turkestan come fossils of stoneflies (*Mesonemura*) belonging to the present-day family TAENIOP-

TERYGIDAE, and many that are known from the Baltic Amber of the Lower Oligocene are little different from living forms.

To sum up, the various lines of the Euplecoptera, arisen no doubt from Gondwanian stocks, seem to have evolved continuously from Permian times down to the present day.

18. Order **Notoptera**. These strange and very primitive insects, which are still to be found in the Rocky Mountains (*Grylloblatta*) and in Japan (*Ischiana*) are certainly survivors from a very ancient stock, but there is no fossil evidence to tell us their history.

19. Order **Phasmoptera**. The Phasmids are a big group of cursorial Orthoptera which in the Jurassic underwent a period of great expansion, and which is still strongly represented in the fauna of tropical countries, but its origin is still in doubt. It seems possible for them to have been derived from primitive Protorthoptera, but the intermediate links are missing. Handlirsch has put several Palaeozoic fossils into the ancestry of the Phasmids, such as *Protophasma dumasi*, which we have mentioned above, and which we have seen really belongs to the Protoblattoptera. The descent of some of his groups from the Phasmoptera is still possible, though it has not been proved. This is also true of the next two Sub-Orders to be mentioned, which are placed here only with reservations.

Sub-Order *Caloneuroidea*

The several families of this group bring together fossils from the Upper Carboniferous of Comenstry and the Permian of Kansas and of Russia. The wing-venation resembles that of the Protorthoptera, but in sharp contrast to the specialized venation we have the fact that the wings are almost alike.

Sub-Order *Glosselytroidea*

This group of cursorial Orthopteroid forms is known from the Upper Permian of Russia, and was defined by Martynov. They have precostal veins like the primitive Orthoptera (*Oedischia*), and certain other venational details are reminiscent of the Orthoptera Saltatoria.

Sub-Order *Phasmoidea*

This is the group that includes the living Phasmida. During the Mesozoic it seems to have passed through a phase of very active radiation, at any rate if the various wings that have been assigned to it really belong to the Phasmoptera. Families of very diverse character have been placed here—CHRESMODIDAE, NECROPHASMIDAE, AEROPLANIDAE, etc.—but unfortunately the fossils concerned are often fragmentary.

All these families flourished in the Jurassic, but their ancestry in the

PLATE 3—X. PLECOPTERA, PHASMOPTERA
AND ORTHOPTERA

A. *Lemmatophora typica* SELL. (Lemmatophoridae),
four times natural size, from the Lower Permian of
Elmo, Kansas.

B. *Permocapnia brevipes* MART. (Permocapniidae),
twice natural size, from the Upper Permian in Russia.

C. *Chresmoda obscura* GERM. (Chresmodidae), two-
thirds natural size, from the Upper Jurassic of Bavaria.

D. *Oedischia williamsoni* BRONGN. (Oedischiidae),
two-thirds natural size, from the Upper Carboniferous
of Commentry, Allier.

E. *Metoedischia* sp. (Oedischiidae), natural size, from
the Upper Permian in Russia.

F. *Elcana* sp. (Elcanidae), enlarged by one-half, from
the Upper Lias of Mecklenburg.

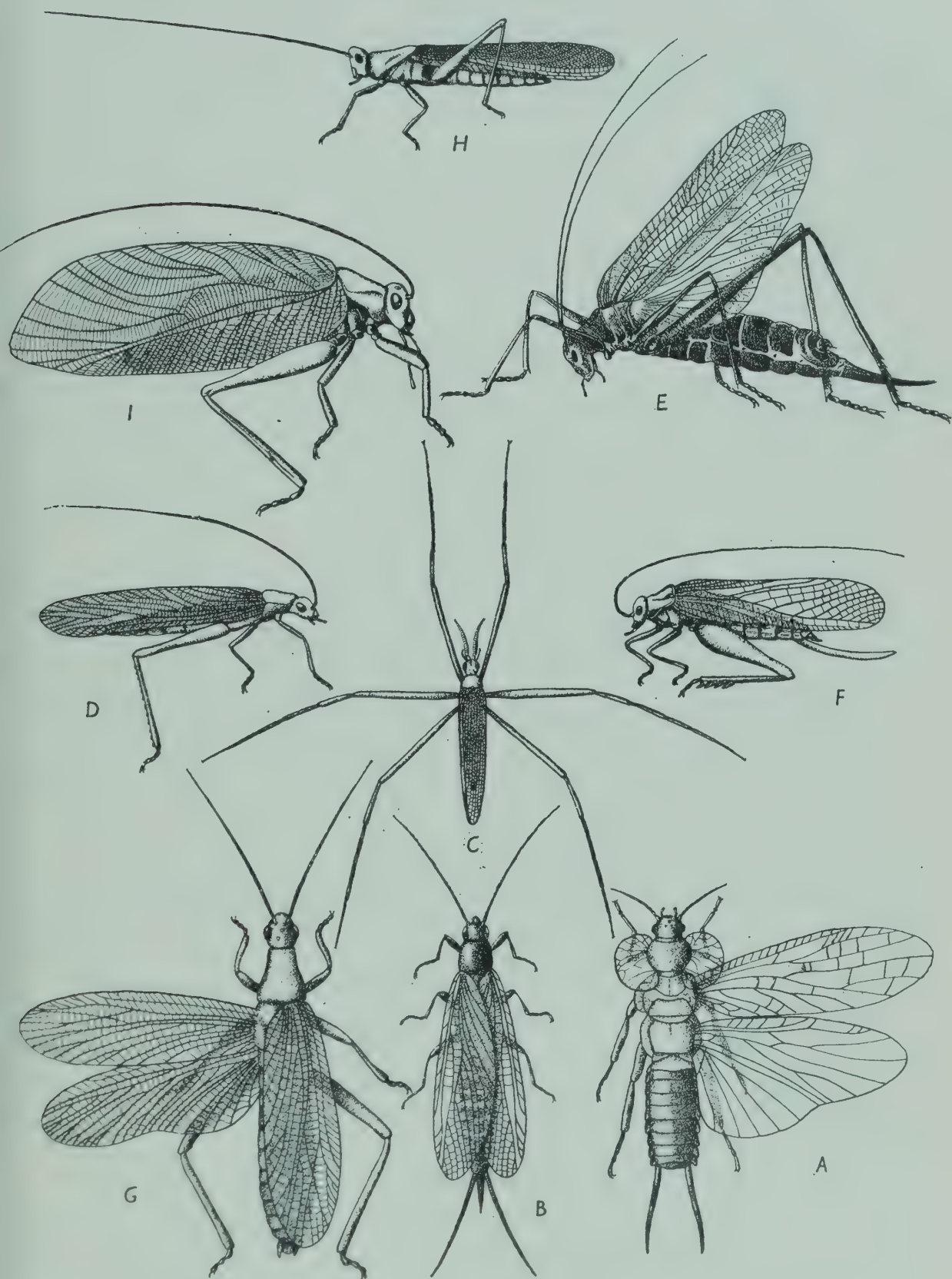
G. *Sthenaropoda fischeri* BRONGN. (Sthenaropodidae), two-thirds natural size, from the Upper Carboniferous of Commentry, Allier.

H. *Conocephalopsis capito* DEICHM. (Locustopsidae),
two-thirds natural size, from the Upper Jurassic of
Bavaria.

I. *Cyrtophyllites rogeri* OPP. (Tettigoniidae), two-
thirds natural size, from the Upper Jurassic of Bavaria.

(Figs. A, B and E after MARTYNOV, the others after
reconstructions by HANDLIRSCH.)

PLATE 3 - X. PLECOPTERA, PHASMOPTERA
AND ORTHOPTERA



Palaeozoic is not known. Only one of them need be mentioned, and that is the best known.

Family CHRESMODIDAE Handlirsch. Handlirsch was struck by the peculiar appearance of a fossil from the Upper Jurassic of Bavaria, showing an insect with long legs and of such a shape that he thought it must be a water-strider, like the living *Gerris* and *Hydrometra*. Martynov has demonstrated that it is nothing of the kind, and is only a Phasmid with unusually long legs.

Chresmoda obscura Germ., from the Upper Jurassic of Bavaria. Pl. 3, X (C).

The Family PHASMIDAE, including the living forms, has also representatives in the Baltic Amber (Upper Oligocene) and in the Miocene of Florissant, Colorado.

20. Order **Orthoptera**. These saltatorial insects, which are so widely distributed in the living fauna, and are divided into the three great groups of Tettigonioidea, Grylloidea and Acridioidea, have left very few traces in the fossil record. We know very little about their origin, but we must assume that they go back to the Palaeozoic.

Sub-Order *Tettigonioidea*

A certain number of extinct families can be placed in direct ancestry to the living forms: their affinities have been disputed, but these fossils do seem to have been antecedents of all the Orthoptera Saltatoria. Outside the TETTIGONIIDAE, none of the rest seem to have had stridulating organs.

Family OEDISCHIIDAE Handlirsch. These Orthoptera were common in the Upper Carboniferous. They were long-horned grasshoppers like those of the present day, but still with prognathous head, and with primitive wing-venation, including a precostal field. The hind-legs, however, were already adapted for jumping.

Seven genera are known, two from North America and five from Europe, from the Carboniferous strata. Permian fossils have been found in Germany and in Russia. Examples:

Oedischia williamsoni Brongn., from the Stephanian of Commentry. Pl. 3, X (D).

Metoedischia sp., from the Permian of Russia. Pl. 3, X (E).

Family ELCANIDAE Handlirsch. Closely related to the last family, and clearly belonging to a collateral branch, the ELCANIDAE arose in the Mesozoic and became extinct in the Eocene. Example:

Elcana sp., from the Upper Lias of Mecklenburg. Pl. 3, X (F).

Family STHENAROPODIDAE Handlirsch. This family, like the Oedischiidae, was placed by Handlirsch in the Protorthoptera. The general appearance is indeed very much the same, but the two pairs of wings have

the same length, there is a precostal field, and above all, the great development of the hing-legs indicates that they were specialized for jumping. There was no stridulating organ.

One genus, *Sthenaropoda*, has two species in the Upper Carboniferous of France; another genus, *Permacoidites*, was described by Martynov from the Upper Permian of the River Sojana, near Archangel. Example:

Sthenaropoda fischeri Brongn., from the Stephanian of Commentry. Pl. 3, X (G).

Martynov considers that the Carboniferous stock of the STHENAROPODIDAE gave rise, on the one hand to the Hagloidea (Hagloidea), a group which flourished at the beginning of the Mesozoic, which had stridulatory organs, and from which the GRYLLACRIDIDAE are said to have arisen; and on the other hand to the stem of the TETTIGONIIDAE.

Family LOCUSTOPSIDAE Handlirsch. Orthoptera of an elongate shape, with a carinate prothorax quite like that of ACRIDIDAE, but with the long antennae of the TETTIGONIIDAE, and wings without stridulating mechanisms. The family flourished in the Jurassic, in Europe and in Siberia. Example:

Conocephalopsis capito Deichm., from the Upper Jurassic of Bavaria. Pl. 3, X (H).

Family TETTIGONIIDAE Kirby (LOCUSTIDAE Steph.). This great group, which is abundant at the present time, has existed since the Jurassic. We have seen that Martynov would derive them from the Hagloidea, in which the stridulating organs were already developed, and through these would relate them to the STHENAROPODIDAE of the Carboniferous. Example:

Cyrtophyllites rogeri Opp., from the Upper Jurassic of Bavaria. Pl. 3, X (I).

Sub-Order *Acridioidea*

No fossil Acridioidea are known from the Mesozoic, but they appear in some numbers in the Tertiary, mostly in the Oligocene and Miocene deposits.

Now, it cannot be doubted that locusts must have had ancestors during the Mesozoic, and their absence from the deposits of the Northern Hemisphere can only be explained by supposing that the evolution of this group took place in Gondwanaland, where the fossil-bearing deposits are much rarer, and where no traces of the Acridioidea have been preserved for us.

If this hypothesis is true, the Acridioidea, and more particularly the migratory ones, must have had a world-wide distribution during the Montian, at the same period as all the innumerable insect lines of the Gondwanian fauna that crossed the Mediterranean Sea in that epoch.

21. Order **Embioptera**. Palaeozoic Embioptera have only recently been discovered. It was not till 1937 that Tillyard recorded *Protembia permiana* from the Lower Permian of Kansas. The wing of this insect is very like that of living Embioptera of the more primitive genera, such as *Clothoda*, but certain details of venation show that it does not lie in direct ancestry to the living forms. The PROTEMBIIDAE are yet another group of carboniferous insects that became extinct without leaving descendants, and were replaced by forms arriving from elsewhere.

Fossil Embioptera are known from a number of Tertiary deposits. The genus *Oligotoma* has been found occasionally in the Baltic Amber, and in the Miocene of Colorado.

Superorder DERMAPTEROIDEA

Two Orders are brought together here, a fossil one—Protelytroptera, now extinct—and a living one, the Dermaptera, or Earwigs. They have in common the following characters: fore-wings transformed into elytra; hind-wings with a broad neala, which folds like a fan and is hidden under the elytra.

22. Order **Protelytroptera**. The Protelytroptera are perhaps the most remarkable of the insect fossils to be found in the deposits at Elmo, in Kansas. They were small insects, with cerci that were segmented, but short, like those of the cockroaches. The tarsi were five-segmented. The fore-wing had the shape of an elytron, but was not shortened, and was flat, with a reduced venation. The hind-wing folded like a fan.

Tillyard rightly compared these with Dermaptera, and concluded that they could be ancestral to the earwigs of the Mesozoic, such as *Protodiplatys*, which had five-segmented tarsi and had pincers instead of cerci. The second point cannot be substantiated; the Protelytroptera were really an independent line, perhaps arising from the Carboniferous cockroaches, which, like to many others, became extinct at the end of the Palaeozoic without leaving descendants.

The Protelytroptera appeared in the Lower Permian in Kansas, and have been found also in the Russian deposits. Following Carpenter, we include along with these the Protocoleoptera that Tillyard described from the Upper Permian of Australia, and which we treat as simply a family of the Protelytroptera.

The known fossils are numerous and well preserved, and can be grouped into several families.

Family ELYTRONEURIDAE Carpenter. These were the most primitive species, and had very flat elytra, without a marginal vein. The venation is close to that of the cockroaches, some of which had true elytra, e.g. *Scutinoblatta* Scudd.

Family MEGELYTRIDAE Carpenter. Here the marginal vein is fore-shadowed, and the distal part of the wing is reticulate.

Family PROTELYTRIDAE Carpenter. The elytra have a well-developed marginal vein, enveloping the entire hind margin; the anterior cubital vein is simple. Example:

Protelytron permianum Carp., from the Lower Permian of Kansas. Pl. 3, XI (A).

Family ARCHELYTRIDAE Carpenter. The characters are the same, except that the anterior cubital vein is bifurcate.

Family BLATTELYTRIDAE Carpenter. The most highly-evolved group of the Kansas fauna, in which the venation of the elytra is almost entirely lost.

Family PROTOCOLEIDAE Tillyard. This family was described by Tillyard, who considered it as consisting of primitive Coleoptera, and erected the Order Protocoleoptera for it.

The fossil was a print of a wing 24 mm. long, with a very complete venation, but having the appearance of an elytron. Tillyard called it *Protocoleus mitchelli*. Later on the same author added his genus *Permofulgor*, with a more sparse venation, which he had at first taken for a Homopteron. *Protocoleus* and *Permofulgor* belong to the fauna of Bel-

Fig. 130 – Left elytron of *Protocoleus mitchelli* TILLYARD, a Protelytropheron from the Upper Permian of Belmont, Australia (after TILLYARD).



mont, New South Wales—that is, to the Upper Permian. Finally, Martynov discovered another wing of great size in the Upper Permian of Archangel, which he made the type of the genus *Arctocoleus* Mart. Fig. 130 shows an elytron of:

Protocoleus mitchelli Till.

As thus composed, the order Protelytrophera is thus to be seen as a

great Gondwanian group, the origins of which go back to the Carboniferous, and which came into view at the two opposite sides of Laurentia, first in Kansas during the Lower Permian, and then in Russia during the Upper Permian (*Arctocoleus*).

23. Order **Dermaptera**. The oldest known Dermaptera date back to the Jurassic.

Family PROTODIPLATYIDAE Martynov. Fossil imprints of these insects were discovered in the Middle Jurassic of Turkestan, and described by Martynov. The cerci of *Protodiplatys* were long and many-segmented, still retaining the character of those of the stoneflies; in contrast, those of *Semenoviola* were already modified into pincers.

Family FORFICULIDAE Stephens. Species of the genus *Forficula* have been found as fossils in the Middle Eocene in Italy, the Lower Oligocene of Aix-en-Provence, and in the Lower Oligocene of the Baltic Amber. In America, Scudder has described several Miocene species from Florissant, Colorado, which he placed in a special genus, *Labiduromma*. Example.

Labiduromma exsulatum Scudd., from the Miocene of Colorado. Pl. 3, XI (B).

C. SECTION OLIGONEOPTERA

Superorder COLEOPTEROIDEA

24. Order **Coleoptera**. We have seen above that the Protocoleoptera of Tillyard are not in any way direct ancestors of the Coleoptera, but the same cannot be said of other fossil imprints in the same Australian and Russian deposits. These are really the remains of primitive Coleoptera, and would have been more appropriately named 'Protocoleoptera', but as this name has been used, the name 'Archicoleoptera' is here given to them.

The Archicoleoptera of the Permian

These can be arranged in several families, all extinct. As P. de Peyerimhoff pointed out, the Archicoleoptera are absolutely characterized by not yet having developed the 'humeral callus', the concave projection of the shoulder of the elytron formed from the base of the epipleuron and covering over the articulation of the membranous hind-wing. The absence of a humeral callus shows that the elytra had not yet become specialized for their function as sheaths when at rest, and stabilizers when in flight; they were still simple 'tegmina' like those of the cockroaches, beating the air in flight like true wings. Moreover, the wing-venation of the elytra was still irregular, and was a long way from settling down into the nine

very regular striae that the true Coleoptera have. These Archicoleoptera are known only from poorly preserved imprints of wings.

Family PERMOSYNIDAE Tillyard. Known from imprints of very small elytra, with the venation more or less reticulate.

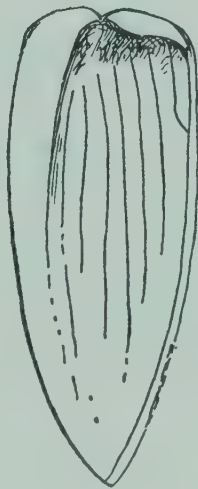
Permosyne and *Permophilus* from the Upper Permian of Belmont, New South Wales, and *Adenosyne* from the Upper Trias of Ipswich, Queensland, were supposed by Tillyard to be in the line of descent of the HYDROPHILIDAE, but there is no foundation for this hypothesis. Martynov added to the PERMOSYNIDAE a species of a bigger size, the elytron of which was found in the Upper Permian of Iva Gora, Archangel. The elytron of *Permocrossos elongatus* Mart. gives a good impression of being the wing of a beetle, though with a venation simpler than that of the Australian forms, an epipleura already modified, and a recognizable 'juxtascutellary striole'.

Permocrossos elongatus Mart. Fig 131 shows the left elytron of this species.

Families PERMARRHAPHIDAE Martynov and SOJANOCOLEIDAE Martynov. The elytron in these families of Archicoleoptera shows a strong resemblance to that of living *Arrhaphipterus*, of the Family RHIPICERIDAE, having the same reticulate sculpture, the same proportions, but without the humeral callus. *Permarrhaphus venosus* Mart. and *Sojanocoleus reticulatus* Mart. comes from the Upper Permian of Tikhie Gory, in the Russian province of Kazan.

Sojanocoleus reticulatus Mart. Fig. 132 shows the right elytron of this species.

Fig. 131—Left elytron of *Permocrossos elongatus* MART., Archicoleopteron of the Upper Permian of Archangel, Russia (after MARTYNOV).



Sub-Order *Archostemata*

All the elytra discussed so far in this group have been attributed to primitive Coleoptera, which have been provisionally grouped into the Archicoleoptera, until complete insects are discovered, and will enable

us to decide whether they are true Coleoptera, or a distinct more primitive Order. But along with these remains of Archicoleoptera, the Permian of Russia also yields traces of true Coleoptera, and it is noteworthy that these belong to the *Archostemata*, which is rightly looked upon as being the most primitive in the Order.

Family CUPEDIDAE Lacordaire. There is no longer any doubt about *Permocupes semenovi* Mart., or *Permocupoides distinctus* Mart., which

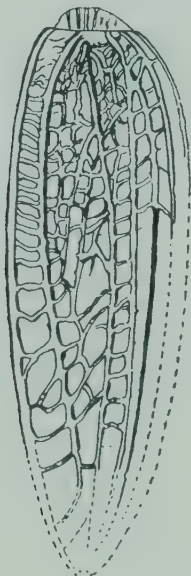


Fig. 132 – Right elytron of *Sojamocoleus reticulatus* MART., an Archicoleopteron of the Upper Permian of Tikhie Gory, Russia (after MARTYNOV).

are known from imprints of elytra in the Upper Permian of Tikhie Gory; they are undeniably remains of CUPEDIDAE. The same is no doubt true of an even older imprint, found in the Lower Permian in the Urals, which Rohdendorf has described under the name of *Tshekardocoleus magnus* (C.R. Ac. Sc. U.R.S.S., 1944, p. 252). Examples:

Permocupoides distinctus Mart., from Tikhie Gory. Fig. 133.

Tshekardocoleus magnus Rohd., from the Lower Permian of Tshekarda, in the Urals. Fig. 134.

It is remarkable to find true Coleoptera existing in Russian deposits from the beginning of the Permian. Everything that has been said already about the origin of the Permian fauna is consistent with the idea that the Coleoptera, like all the Holometabola, originated in Gondwanaland.

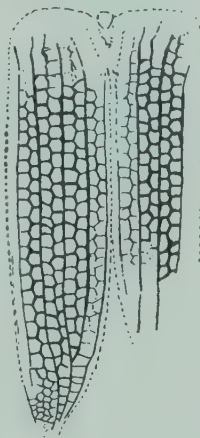
The Other Sub-Orders of Coleoptera

Remains of beetles are found abundantly in deposits throughout the Mesozoic and Tertiary Eras, but unfortunately very few of them can be identified with certainty. Out of about five hundred fossil imprints that have been given the names of species, genera and families, the ones that an expert entomologist could recognize again with confidence are very

few. All that can be said is that Carabids, Hydrophilids, Buprestids and Chrysomelids made an early appearance in the fauna of the Mesozoic.

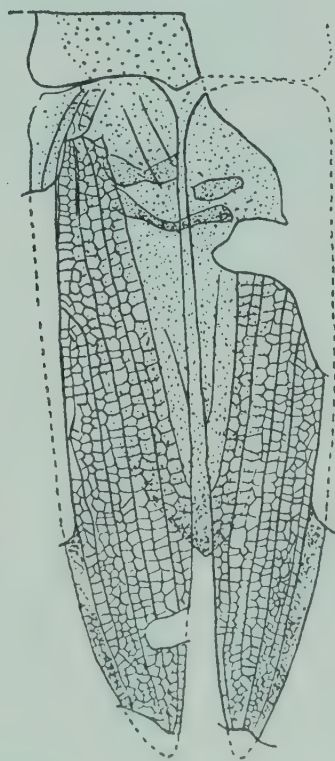
The majority of the carnivorous, wood-feeding, or saprophagous

Fig. 133 – Elytra of *Permocupoides distinctus* MART., a Cupedid beetle from the Upper Permian of Tikhie Gory, Russia (after MARTYNOV).



groups that are present among the beetles of today had already made their appearance in the Jurassic. Most of the phytophagous, leaf-living, or flower-feeding groups, however, did not appear until Cretaceous or Tertiary times, arriving no doubt with the Angarian fauna. The Baltic

Fig. 134 – Elytra of *Tshekardocoleus magnus* Rohd., a Cupedid beetle from the Lower Permian of Tshekarda, Ural (after ROHDENDORF).



Amber, which dates from the Lower Oligocene, has yielded a very rich beetle-fauna, the specimens of which are perfectly preserved for identification. All of them are heat-loving forms, mostly identical with genera still

PLATE 3 – XI. PROTELYTROPTERA, DERMAPTERA,
COLEOPTERA, RAPHDIOPTERA & PLANIPENNIA

A. *Protelytron permianum* CARP. (Protelytridae), enlarged,
from the Lower Permian of Elmo, Kansas.

B. *Labiduromma exsulatum* SCUDDER (Forficulidae),
twice natural size, from the Miocene of Colorado.

C. *Palaeognathus succini* WAGA. (Chiasognathidae), natural
size, from the Baltic Amber.

D. *Inocellia erigena* HAGEN (Raphidiidae), twice natural
size, from the Baltic Amber.

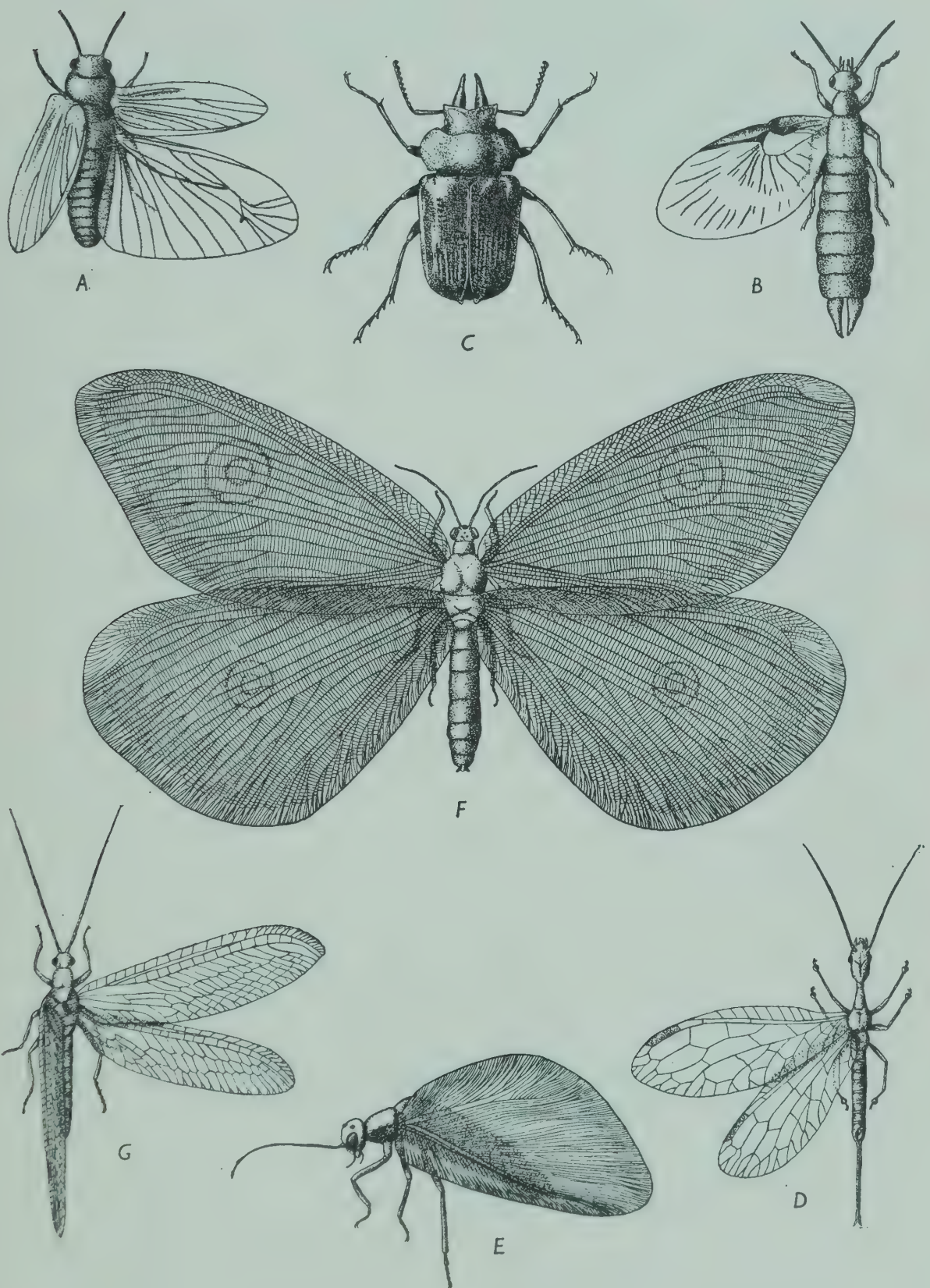
E. *Mesopsychopsis hospes* GERM. (Hemerobiidae), enlarged
by one half, from the Upper Jurassic of Bavaria.

F. *Kalligramma haeckeli* WALT. (Kalligrammatidae), one-
half natural size, from the Upper Jurassic of Bavaria.

G. *Mesochrysopa zitteli* MEUN, natural size, from the
Upper Jurassic of Bavaria.

(Fig. A after CARPENTER; the others after reconstructions
by HANDLIRSCH.)

PLATE 3 - XI. PROTELYTROPTERA, DERMAPTERA,
COLEOPTERA, RAPHDIOPTERA & PLANIPENNIA



in existence, but no longer to be found in Northern Europe. Today they exist only in the tropics, mainly in America.

CYCHRITIDAE of the genus *Nomaretus*, present today in North America, occurs in the Baltic Amber. The CICINDELIDAE of the Amber include *Tetracha carolina*, now found in the southern United States; and the Amber has also yielded CUPEDIDAE of the genus *Triacma*, still found in America, and PAUSSIDAE, ZUPHIIDAE and ANTHIIDAE, all belonging to groups still found in the tropics. LAMPYRIDAE (fireflies) BUPRESTIDAE and CURCULIONIDAE are also found in the Amber and in the modern tropics.

Finally, there have been found in the Baltic Amber representatives of groups that today have a subantarctic distribution, in South America, the southern tip of Africa, and Australia. An example of this is a *Chiasognathus*, of the family LUCANIDAE.

Palaeognathus succini Waga., from the Baltic Amber, is illustrated in Pl. 3, XI (C).

Superorder NEUROPTERA

25. Order **Megaloptera**. We know little enough about the origin of the Megaloptera, but they are no doubt descended from a Gondwanian stock in common with the Mecoptera. Although they are few in number at the present day, they seem to have been much more abundant in earlier periods. The living species are divided into two families, SIALIDAE and CORYDALIDAE, of which the former was preceded by several other families now extinct, but with a history going back to the Permian.

Family MARTYNOVIDAE Tillyard. These Sialidoidea had a wing-venation in which can be seen the main characters of the SIALIDAE, but with a union between veins RS and M which is not found in any living group of this Order. The MARTYNOVIDAE were found in the Lower Permian of Kansas.

Families PERMOSIALIDAE Martynov and ARCHISIALIDAE Martynov. Wings with a reduced venation, evolved as far as that of *Sialis*; the PERMOSIALIDAE with Cu independent of M, but the ARCHISIALIDAE with Cu and M forked together, as in the modern SIALIDAE, to which the ARCHISIALIDAE could be direct ancestors. Both families are known from fossil imprints of wings in the Upper Permian of the provinces of Kazan and Archangel.

Family CHAULIODITIDAE Handlirsch. Here are placed some imprints of wings taken from the Trias of Gödewitz, in Saxony. The wing of *Chauliodites picteti* Heer indicates the line of ancestry of *Chauliodes*, which survives at the present time, and belongs to the family CORYDALIDAE.

Finally, true SIALIDAE (*Sembris*) and CORYDALIDAE (*Chauliodes*) are known from the Baltic Amber.

26. Order **Raphidioptera**. Hardly any more is known about the origins of this Order, which at the present time is represented by the family RAPHIDIIDAE. The PERMORAPHIDIIDAE, described by Tillyard from the Lower Permian of Kansas, seem to fall into direct ancestry with the RAPHIDIIDAE. They are continued into the Jurassic as the MESORRAPHIDIIDAE, with a genus *Mesorraphida* which Martynov erected for five species that are known from imprints of wings in Turkestan. RAPHIDIIDAE are known from the Baltic Amber. Example:

Inocellia erigena Hag., from the Baltic Amber. Pl. 3, XI (D).

27. Order **Planipennia**. The wings of the true Neuroptera, or Planipennia, are remarkable for their very rich and much branched venation, notably the radial sector, though there is a simple venation in *Coniopteryx*. The Psocoptera, which are not known as fossils, are close to the Planipennia, and seem clearly to have arisen from a primitive group of HEMEROBIIDAE, by secondary simplification.

Leaving out the CONIOPTERYGIDAE, the Planipennia fall into two Sub-Orders, Hemerobioidea and Myrmeleonoidea. The latter are known as fossils only from the Tertiary, but the former appear in the Permian, and during the Mesozoic had a period of extraordinary expansion.

Sub-Order *Hemerobioidea*

Most of the living families have been in existence since the Permian.

Family BEROETHIDAE Handlirsch. *Permoberothe*, described by Tillyard from the Lower Permian of Kansas, is the oldest known member of the Planipennia.

Family SISYRIDAE Handlirsch. This family, in which the venation has remained primitive, had an ancestor *Permosisyra*, which Martynov described from the Upper Permian of Russia.

Family HEMEROBIIDAE Handlirsch. Again from the Upper Permian deposits of Russia, Martynov recorded a series of fossil imprints, from which he described two families, with many genera. He called the families PALAEMEROBIIDAE and PROHEMEROBIIDAE, but in fact these genera are primitive forms that are apparently ancestral HEMEROBIIDAE.

PROHEMEROBIIDAE have also been found in the Upper Trias of Ipswich, in Australia, then in the Lias of England and of Mecklenburg, the Lias of the Urals (*Archegetes*), and the Upper Jurassic of Bavaria (*Mesopsychopsis*). This is the distribution appropriate to a Gondwanian line that has been dispersed throughout the Northern Hemisphere by migrations during the Mesozoic. Example:

Mesopsychopsis hospes Germ., from the Upper Jurassic of Bavaria. Pl. 3, XI (E).

Family PSYCHOPSIDAE Handlirsch. Localized in the Australian Region, this family has been there since the Trias; according to Tillyard, *Triassopsychops superba* Till., from the Upper Trias of Ipswich, was a direct ancestor of *Megapsychops illidgei* Frogg., which can be seen in flight today scarcely fifty miles away from the spot in which the fossil was found.

Triassopsychops superba Till. The left fore-wing of this species is shown in Fig. 135.

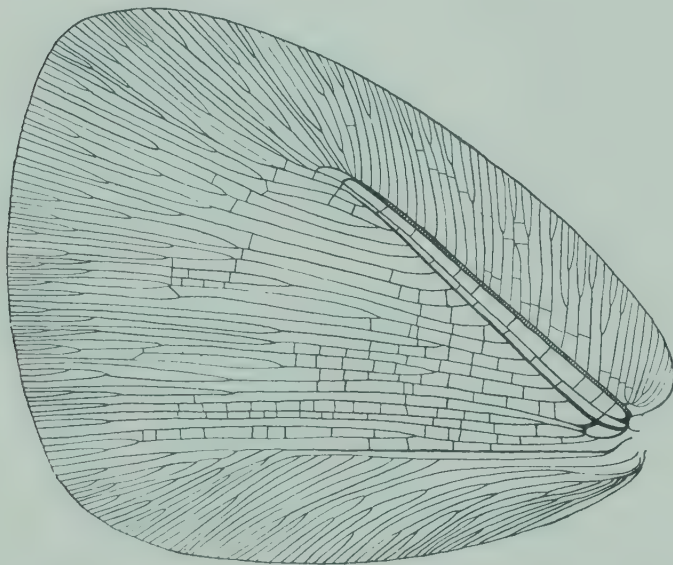


Fig. 135 – Left fore-wing of *Triassopsychops superba* TILLYARD, one of the Planipennia from the Upper Trias of Ipswich, Australia (after TILLYARD).

Family KALLIGRAMMATIDAE Handlirsch. In the European Jurassic there were several families of Planipennia that are extinct today, but which are certainly allied to the Psychopsidae of Australia. Among others there are the SOLENOPTILIDAE and the KALLIGRAMMATIDAE. The latter were big, brilliantly coloured, the wings patterned with eyespots, and in the Jurassic period they occupied the place that butterflies occupy in the fauna of the present day. The living PSYCHOPSIDAE, still big and butterfly-like, show what the KALLIGRAMMATIDAE must have been like in their day. Example:

Kalligramma haeckeli Walt., from the Upper Jurassic of Bavaria. Pl. 3, XI (F).

Family CHRYSOPIDAE Handlirsch. One genus from the Upper Jurassic, *Mesochrysopa*, placed by palaeontologists in a special family, the MESOCHRYSOPIDAE is apparently a precursor of the living CHRYSOPIDAE. Example:

Mesochrysopa zitteli Meun., from the Upper Jurassic of Bavaria. Pl. 3, XI (G).

Family ITHONIDAE Tillyard. An Australian group which occupies an isolated position in the Sub-Order Hemerobioidea. Tillyard has recorded a fossil with wings of the same narrow shape from the Upper Permian of Belmont, New South Wales. At the same time this fossil, *Permithone belmontensis* Till. shows certain affinities with the PALAEMEROBIIDAE of the Russian deposits of the same Period.

The families OSMYLIDAE and MANTISPIDAE are not known as fossils.

Thus we see that the Hemerobioidea originated in Gondwanaland, and were already specialized in the Permian. They were distributed throughout Laurentia in the Mesozoic and were particularly successful there in the Jurassic, when they took the place of butterflies on the world stage. Their period of dominance came to an end in the Cretaceous, and the living representatives are but a poor shadow of those of the Jurassic.

Sub-Order *Myrmeleonoidea*

Several species of *Myrmeleon* are known from the Baltic Amber; and *Ascalaphus* has been found in the Lower Miocene of Puy, in France; and finally, a very fine Nemopterid, *Halter americanus* Cock. has been described from the Miocene of Florissant, in Colorado.

Superorder MECOPTEROIDEA

This group has also been called 'Petanoptera' by Lameere, and 'Panorpoidea' by Tillyard. It is centred round the Mecoptera, with which it links, on the one hand the Trichoptera and Lepidoptera, and on the other the Diptera.

28. Order **Mecoptera**. The first Mecoptera appeared in the Permian; they are occasionally found in the Lower Permian of Kansas, and in the Upper Permian of Australia and of Russia, in such a way that they have the appearance of having arisen in Gondwanaland, and been early immigrants to the Laurentian asylum of the Northern Hemisphere. Their interest lies in the light they throw on the various living Orders that are grouped together as Mesopteroidea.

The living Mecoptera group round the two main families, PANORPIDAE and BITTACIDAE. The primitive forms that came before them have been arranged by Tillyard into a number of families, now extinct, and which he grouped into several Sub-Orders. Two of these Sub-Orders consist of Mecopteran lines that have led on to the living genera; a third, the Paramecoptera, is an artificial grouping from which the Trichoptera and the Diptera can be derived.

Sub-Order *Eumecoptera*

These are the Mecoptera proper, and were abundant in the Lower Permian.

Family PERMOCHORISTIDAE Tillyard. This family has a few representatives in the Lower Permian of Kansas, and the Upper Permian of Australia and of Russia, and persists into the Upper Trias of Ipswich. The same genera turn up in these scattered deposits.

The imprints of wings that are known fall into about thirty genera, and belong to scorpion-flies that are small by modern standards. Those of the Trias of Ipswich seem to have been the stem from which came the

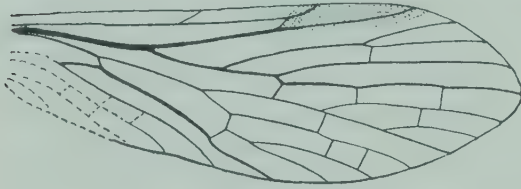


Fig. 136. – Right fore-wing of *Permochorista sinuata* TILLYARD, a Mecopteron from the Upper Permian of Belmont, Australia (after TILLYARD).

CHORISTIDAE and the NANNOCHORISTIDAE of the present fauna of Australia and New Zealand.

To the PERMOCHORISTIDAE are allied the ORTHOPHLEBIIDAE with a dozen genera known from the Jurassic of Europe and Siberia, and which were precursors of our modern PANORPIDAE. Example:

Permochorista sinuata Till., from the Upper Permian of Belmont, Australia. The right fore-wing of this species is shown in Fig. 136.

Family PLATYCHORISTIDAE Tillyard. Another major line, known only from the Lower Permian of Kansas, and which had the precostal field of the wing covered with a network of veins. The living MEROPEIDAE could be their descendants.

All these ancient stocks have been succeeded in Tertiary times by the PANORPIDAE, BITTACIDAE and MEROPEIDAE, whose remains are known from the Baltic Amber and from the Miocene of Croatia and of Colorado.

Sub-Order *Protomecoptera*

Family ARCHIPANORPIDAE Tillyard. Tillyard erected this Order and this family for one well-preserved wing from the Upper Trias of Ipswich. This *Archipanorpa magnifica* Till. was the direct ancestor of *Notiothauma reedi*, a living scorpion-fly of Chile, and as an Australian fossil of the Trias, shows that *Notiothauma* is a relict from a very old Palaeantarctic line.

Sub-Order *Paramecoptera*

Tillyard founded this Sub-Order for two fossil wings from the Upper Permian of Belmont, New South Wales: *Belmontia mitchelli* Till. and *Parabelmontia permiana* Till.

Belmontia, with the cubital vein forked, could be ancestral to the Paratrachoptera of the Trias of Ipswich and of the Siberian Lias, which were themselves ancestral to the Trichoptera.

Parabelmontia, with the cubital vein simple, must have been closely allied to *Permotipula*, which was contemporaneous, and which constitutes the Sub-Order Protodiptera, precursors of the Diptera. Example:

Belmontia mitchellii Till., from the Upper Permian of Belmont. The right fore-wing of this species is shown in Fig. 137.

29. Order **Trichoptera**. No true Trichoptera are known earlier than the Lias, but if we follow Tillyard's interpretations of the wings of the Paramecoptera we must look for the ancestors of the Trichoptera in Australia; according to him, the Paramecopteran *Belmontia* was at the origin of the primitive Trichoptera (Sub-Order Paratrachoptera) which abounded in the Upper Triassic deposits of Ipswich. From these Paratrachoptera arose the Trichoptera and then, secondarily, the Lepidoptera.

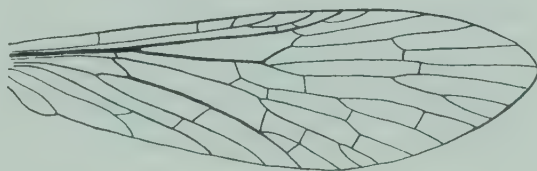
The Trichoptera of the Mesozoic fall into several extinct families.

Family NECROTAULIDAE Handlirsch. Species of very small size, from the Upper Lias and the Jurassic of England and of Mecklenburg. Lameere thought that this family was a heterogeneous mixture, largely composed of members really belonging to the family RHYACOPHILIDAE, but whether that is so or not they all belong to the group Annulipalpa.

Family PROSEPIDIDONTIDAE Handlirsch. A closely allied group, but consisting of much bigger insects, known from the Upper Lias of Mecklenburg.

The cases of caddis-fly larvae are found as fossils only from the end of the Cretaceous, which leads us to suppose that the Jurassic Trichoptera that we have just been discussing cannot have developed these remarkable specializations as we know them in the living forms.

Fig. 137 – Right fore-wing of *Belmontia mitchellii* TILLYARD, a Paramecopteran from the Upper Permian of Belmont, Australia (after TILLYARD).



Trichoptera are found in the Baltic Amber, and one of these deserves special mention. It is a Leptocerid of the genus *Triplectides*, which shows almost the same Palaeantarctic distribution as the Chiasognathid beetles that have been mentioned earlier. It is found in South America, Australia and New Zealand. Like *Palaeognathus succini*, this caddis-fly from the Amber shows that in the warm Oligocene Period the Palaeantarctic fauna spread right up to the North of Europe.

30. Order **Lepidoptera**. It can be said that the origins of the Lepidoptera are completely unknown. The present-day distribution of certain genera in Inabresia—that of the *Castniidae*, for instance—implies that their

ancestry goes far back into the Mesozoic, but no authenticated fossil of a member of the Lepidoptera is known before the Eocene. The Palaeontinidae, which Handlirsch attached to the Lepidoptera, are really Homoptera.

This absence of fossil evidence is understandable if the Lepidoptera had specialized in Angara Land during the Mesozoic, and did not spread through the rest of the world until the end of the Cretaceous, at the same time as there appeared the Angiosperms, that is the flowering plants. However that may be, the remains of Lepidoptera are quite common in Tertiary deposits; the species are varied, and show all the characteristics of a group that is already an ancient one. Examples:

Dorititis bosniaskii Reb., a Papilionid from the Upper Miocene of Italy. Pl. 3, XII (A).

Prodryas persephone Scudd., a Nymphalid from the Miocene of Colorado. Pl. 3, XII (B).

31. Order **Diptera**. As we have already said when we were talking about the Paramecoptera, it seems likely that the Diptera were derived from Permian stocks of primitive Mecoptera, which became specialized by losing their hind-wings. In fact today we have found traces of four-winged ancestors of the Diptera-Nematocera, for which Tillyard has erected the Sub-Order Protodiptera.

Sub-Order *Protodiptera*

This Sub-Order might equally well be placed among the Mecoptera. It was founded for imprints of wings, and one imprint of a complete insect, found in the Upper Permian of Warner's Bay, New South Wales.

This *Permotipula* had four wings, in almost exactly similar pairs, with venation typically Tipuloid, but the fact that the metanotum was already reduced in size seems to point to the eventual disappearance of the hind pair of wings. Some details of the venation are reminiscent of the TANYDERIDAE, but certain specializations, such as the reduction of the fork of R_2 and R_3 , make it impossible for *Permotipula* to have been a direct ancestor of these. Example:

Permotipula sp., from the Upper Permian of Warner's Bay, New South Wales. Pl. 3, XII (C).

The True Diptera

TANYDERIDAE are to be found in Australian deposits of the Upper Trias, from which we can draw the conclusion that the reduction and disappearance of the hind-wings of Diptera must have taken place between the Upper Permian and the Upper Trias, that is during the Triassic Period itself.

On the other hand, the PTYCHOCERIDAE of the European Lias seem

certainly to be derived from the Triassic TANYDERIDAE, giving good grounds for believing that the great group of the Culiciform Diptera may have arisen in Gondwanaland.

A variety of other families are represented as fossils in Mesozoic deposits. PSYCHODIDAE have been described from the Lias of Siberia, while RHYPHIDAE, BIBIONIDAE and MYCETOPHILIDAE are known from the European Lias.

As for the Brachycera, they must be supposed to have arisen from an ancestor in common with the RHYPHIDAE and BIBIONIDAE. A few primitive Orthorrhapha have left traces in the Mesozoic (e.g. *Protobrachyceron liasinum* Handl., from the Lias), and Rohdendorf has described several extinct families from the Mesozoic of Kara-Tau. The Muscoidea, however, do not begin to appear in European deposits until after the Cretaceous, when, along with the Lepidoptera, they accompany the migration of the flowering plants.

Hundreds of species in Diptera have been found in the Baltic Amber, but for the most part they belong to families that are still in existence. Examples:

Palombolus florigenus Scudd., a Nemestrinid from the Miocene of Colorado. Pl. 3, XII (D).

Glossina oligocena Scudd., a Muscid from the Miocene of Colorado. Pl. 3, XII (E).

Superorder APHANIPTEROIDEA

32. Order **Aphaniptera**. The origin of the fleas is still disputed; they seem most likely to be related to the Diptera, even though some authors prefer to relate them to the Coleoptera, on account of their larval characters.

The earliest fleas are found in the Baltic Amber, and it is noteworthy that they make their appearance there already showing all the adaptive characters of the living species. Thus in Oligocene times, that is some 20 million years ago, when the Mammals had hardly begun to radiate and spread over the earth, there were already fleas in existence that were as highly evolved as those of the present day. There can be no doubt, therefore, that the specialization of the fleas for a parasitic existence must have come into being in association with terrestrial vertebrates that lived before the rise of the Mammals. Example:

Palaeopsylla klebsiana Damp., from the Baltic Amber. Pl. 3, XII (F).

Superorder HYMENOPTEROIDEA

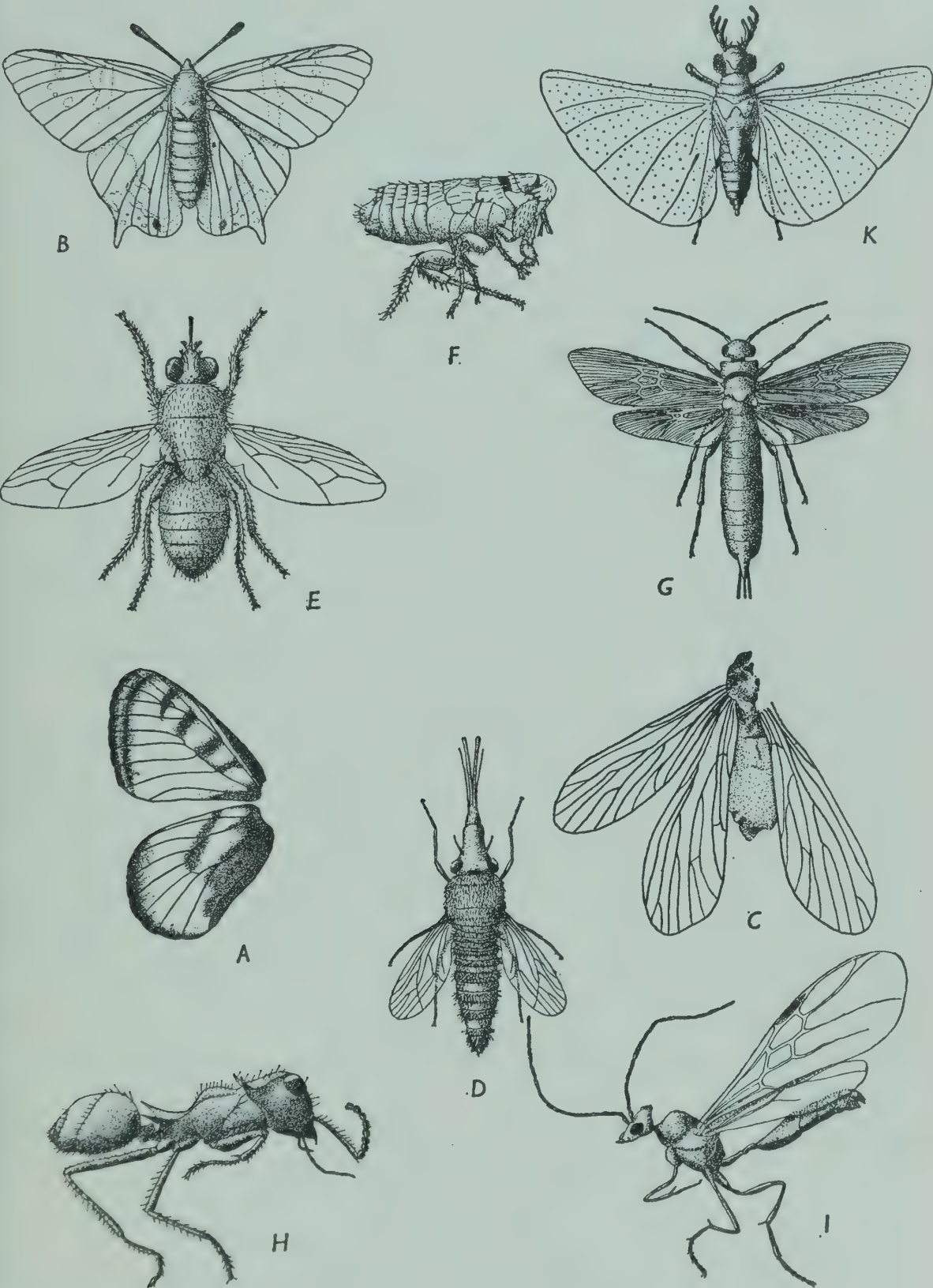
33. Order **Hymenoptera**. The only Mesozoic fossils belonging to this Order are Symphyta. The Parasitica, and above all the Aculeata did not come till much later, along with the flowering plants.

PLATE 3 – XII. LEPIDOPTERA, DIPTERA,
APHANIPTERA, HYMENOPTERA & STREPSIPTERA

- A. **Dorititis bosniaskii** REBEL (Papilionidae), two-thirds natural size, from the Upper Miocene of Italy.
- B. **Prodryas persephone** SCUDDER (Nymphalidae), natural size, from the Miocene of Colorado.
- C. **Permotipula** sp. (Protodiptera), natural size, from the Upper Permian of Warner's Bay, Australia.
- D. **Palombolus florigenus** SCUDDER (Nemestrinidae), enlarged by one-third, from the Miocene of Colorado.
- E. **Glossina oligocena** SCUDDER (Muscidae), enlarged by one-half, from the Miocene of Colorado.
- F. **Palaeopsylla klebsiana** DAMPF (Pulicidae), sixteen times natural size, from the Baltic Amber.
- G. **Pseudosirex** sp. (Siricidae), three-quarters natural size, from the Upper Jurassic of Bavaria.
- H. **Gaesomyrmex corniger** EMERY (Formicidae), seven times natural size, from the Middle Miocene of Sicily.
- I. **Aeromyrma sophiae** EMERY (Myrmicidae), ten times natural size, from the Middle Miocene of Sicily.
- J. **Mengea tertiaria** MENGE (Mengeidae), ten times natural size, from the Baltic Amber.

(Fig. C after TILLYARD; the others after reconstructions by HANDLIRSCH.)

PLATE 3-XII. LEPIDOPTERA, DIPTERA,
APHANIPTERA, HYMENOPTERA & STREPSIPTERA



The oldest known fossil imprint is one of a fore-wing of a Siricoid from the Lower Lias of Shurab, in the Ferghana. Martynov named it *Liadoxyela praecox*, and found in it certain relationships with *Pamphilius* (LYDIDAE), and above all with *Megaxyela* and *Macroxyela* among living forms. Other, more recent imprints have been taken from the Lias of Galkino in Siberia.

On the other hand *Pseudosirex* has been known for a long time, from several species in the lithographic stones of the Upper Jurassic of Solenhofen. These *Pseudosirex* had the look of *Sirex*, but their wing veins were thicker, and were reinforced by a series of fine longitudinal veins more obvious than in living forms. Example:

Pseudosirex sp., from the Upper Jurassic of Bavaria. Pl. 3, XII (G).

The correct placing of *Ephialtes jurassicus* Meun., from the Upper Jurassic of Spain, is uncertain, and it is doubtful whether it is a Hymenopteron at all.

Finally it must be said that there is some evidence that sawflies existed in the Cretaceous; certain imprints of galls, found in Cretaceous deposits in Bohemia, could be attributed to Tenthredinoidea. During the Tertiary there are many fossil Hymenoptera belonging to all the living families. Examples:

Gaesomyrmex corniger Em., a Formicid from the Middle Miocene of Sicily. Pl. 3, XII (H).

Aeromyrma sophiae Em., a Myrmicid from the Middle Miocene of Sicily. Pl. 3, XII (I).

34. Order **Strepsiptera**. It has been established by Jeannel (1944), on morphological grounds, that the Strepsiptera must have arisen from an ancient stock derived from very primitive Hymenoptera. This origin goes back, no doubt to the beginning of the Mesozoic, but there is no fossil evidence to confirm the theory. The oldest known Strepsipteron is *Mengea tertiaria* from the Baltic Amber of the Lower Oligocene. This has been made the type of a family, MENGEIDAE, the most archaic member of the Order, whose living members are parasites of Thysanura. Their larvae are endoparasitic, and are infinitely less degenerate than those of the other families.

Mengea tertiaria Menge., from the Baltic Amber, is illustrated in Pl. 3, XII (J).

D. SECTION PARANEOPTERA

Superorder PSOCOPTEROIDEA.

35. Order **Psocoptera**. A special group, the Permopsocoptera, is used nowadays to bring together a series of imprints of wings or of complete

insects, the systematic position of which used to be much debated. Some (DICHENTOMIDAE) were looked on from the beginning as being primitive Psocoptera, but others (PALAEOMANTIDAE) were at first taken for Phasmids, and others again (ARCHEPSYLLIDAE) for Homoptera.

Family DICHENTOMIDAE Carpenter. Carpenter made a reconstruction of *Dichentomum tinctum*, a tiny insect with a big head, prominent eyes, and antennae with more than fifty segments. The head was drawn out into a rostrum with slender and multi-segmented palpi. The abdomen had ten segments, and no cerci. The wings were homonomous, with a simplified venation, and the tarsi were five-segmented.

These insects are known from fossils in the Lower Permian of Kansas, and several species have been described. Example:

Dichentomum tinctum Till., from the Lower Permian of Kansas. Pl. 3, XIII (A).

Family PALAEOMANTIDAE Martynov. This family combines several species, of which those from the Lower Permian of Kansas have been described as constituting a family DELOPTERIDAE, while others (*Palaeomantis*) come from the Upper Permian of the Archangel District. Martynov showed that Tillyard's DELOPTERIDAE and his own PALAEOMANTIDAE ought to be combined into one family, but he went on to put this family into his own group Miomoptera, near to the Phasmoptera. The Miomoptera later proved to be an artificial group.

Family ARCHEPSYLLIDAE Handlirsch. This is a group that Handlirsch first placed with the Homoptera, but which is really a group of Psocoptera that flourished in the Jurassic. The true Psocoptera must have separated off in an early period, like the stem-groups of the Mallophaga and Anoplura.

Psocoptera of a variety of families are known from the Baltic Amber, while a *Sphaeropsocus* that is very closely related to the following species has only recently been discovered alive:

Sphaeropsocus kunowi Hag., from the Baltic Amber. Pl. 3, XIII (B).

36. Order **Mallophaga**. Not known as fossils.

37. Order **Anoplura**. Not known as fossils.

Superorder THYSANOPTEROIDEA

38. Order **Thysanoptera**. The thrips do not appear as fossils until the Tertiary and their origin is unknown.

The two families THRIPSIDAE and PHLOEOTHIRPSIDAE are represented by various genera in the Oligocene of Colorado, of Aix-en-Provence, and of Transylvania, as well as in the Baltic Amber, and in the Upper Miocene of Oeningen.

PLATE 3 – XIII. PSOCOPTERA, HOMOPTERA
& HETEROPTERA

- A. **Dichentomum tinctum** TILL. (Dichentomidae), enlarged three times, from the Lower Permian of Elmo, Kansas.
- B. **Sphaeropsocus kunowi** HAGEN (Psocidae), thirty times natural size, from the Baltic Amber.
- C. **Permocicada integra** BECK. (Prosbolidae), twice natural size, from the Upper Permian of Archangel, Russia.
- D. **Eocicada microcephala** OPP. (Palaeontinidae), natural size, from the Upper Jurassic of Bavaria.
- E. **Mesonepa minor** HANDL. (Nepidae), natural size, from the Upper Jurassic of Bavaria.
- F. **Mesobelostoma deperditum** GERM. (Belostomatidae), natural size, from the Upper Jurassic of Bavaria.
- G. **Notonecta harnacki** SCHLECHT. (Notonectidae), four times natural size, from the Upper Oligocene of the Rhineland.
- H. **Thanasimosphaeria haasei** HEER. (Scutelleridae), twice natural size, from the Upper Miocene of Baden.
- I. **Aradus superstes** GERM. (Aradidae), four times natural size, from the Baltic Amber.

(Fig. A after TILLYARD; fig. C after MARTYNOV; the others after HANDLIRSCH.)

PLATE 3 - XIII. PSOCOPTERA, HOMOPTERA
& HETEROPTERA



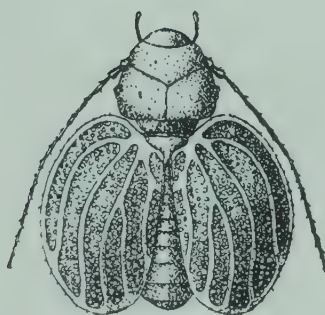
D



C



A



B



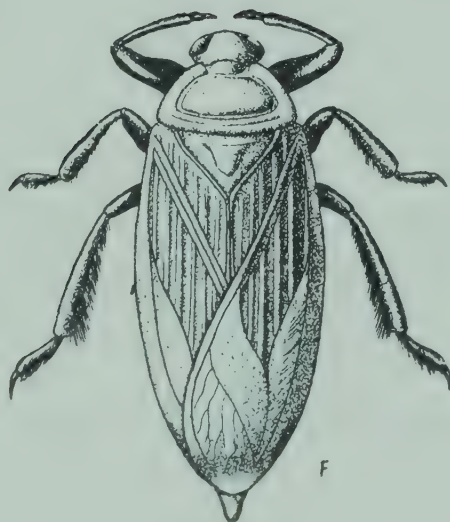
E



G



H



F



I

Superorder HEMIPTEROIDEA

39. Order **Homoptera**. Imprints of the wings of Homoptera have been found in great numbers in the Permian deposits of Kansas, Australia and Russia. Sometimes they are so common that they may make up more than half of the insect remains in a particular deposit. So it seems that in Permian times there was a rich fauna of Homoptera, and there is every reason to believe that it arose in Gondwanaland. No doubt all the Paraneoptera arose in Gondwanaland in the Carboniferous, while Laurentia was populated with Palaeoptera and Polyneoptera.

Living Homoptera are divided into several Sub-Orders, and these in turn are arranged into two Series, Sternorrhyncha (COCCIDAE, ALEURODIDAE, PSYLLIDAE, APHIDIDAE) and Auchenorrhyncha (CERCOPIDAE, JASSIDAE, FULGORIDAE, CICADIDAE). It seems as if these two great groups were derived from another group, more primitive, which lived in the Permo-Triassic Period, and to which Carpenter gave the name 'Palaeorrhyncha'.

The Palaeorrhyncha

Carpenter's ancestral group, which Martynov on the contrary thought was no more than a group of primitive Sternorrhyncha, lived in the Permian, the oldest member known (*Archescytina permiana* Carp.) dating from the Lower Permian of Kansas.

They had the wing-venation of the Auchenorrhyncha, though very primitive, without any of the specializations that appeared among the Auchenorrhyncha of the Permian. Their antennae were long and slender, with about twenty-five segments; that is, of the same type as those of the Sternorrhyncha. On the other hand the wing of *Archescytina* was very much like that of the Permopsocoptera, the only difference being that R_s , which is simple in the Homopteron, was bifurcate in *Dichentomum*.

Palaeorrhyncha have been found in Upper Permian deposits at Belmont, and at Newcastle, in Australia, and were described by Tillyard as *Pincombea mirabilis* and *Lophioneura ustulata*.

The Auchenorrhyncha

Alongside these primitive types, which are classed as Palaeorrhyncha, there appeared in the Upper Permian of Australia and of the Archangel District a host of other imprints of wings, which authors have not hesitated to describe as Auchenorrhyncha. They are primitive types, but they foreshadow a number of living families.

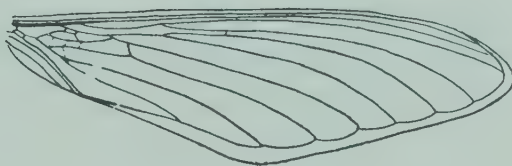
Family PROSBOLIDAE Carpenter. These species have several features in common with the FULGORIDAE, and are known from very many imprints in the Upper Permian of Australia and of Northern Russia. Example:

Permocicada integra Beck., from the Upper Permian of Archangel. Pl. 3, XIII (C).

Family SCYTINOPTERIDAE Tillyard. These Homoptera were precursors of the CERCOPIDAE, and had a venation still more primitive, without a marginal vein. They were common in the Upper Permian of Australia, and again in the Upper Trias of Ipswich. Handlirsch grouped the SCYTINOPTERIDAE with other families that he had described from the Upper Permian of Archangel (COLEOSCYTIDAE, PEREBORIDAE, CICADOPSYLLIDAE) under the name of Palaeohemiptera. These are really Auchenorrhyncha.

Family CIXIIDAE Distant. A living family, that was already differentiated in the Permian, true CIXIIDAE being found in Russian deposits of

Fig. 138 – Right fore-wing of *Mesogereon superbum* TILLYARD, a Homopteron from the Upper Trias of Ipswich, Australia (after TILLYARD).



that period. They appear again in the Upper Trias of Ipswich, accompanied by JASSIDAE, and both families are found in the Lower Lias of Shurab, in Turkestan.

Family IPSWICHIDAE Tillyard. An extinct line, known from the Upper Trias of Ipswich. It may lie in the line of ancestry of the TETTIGOMETRIDAE

Family MESOGEREONIDAE Tillyard. Giant cicadas, with coloured and granulated wings. Example:

Mesogereon superbum Till., from the Upper Trias of Ipswich, illustrated in Fig. 138.

Family PALAEONTINIDAE Handlirsch. Handlirsch has given several reconstructions of these insects, which were of great size. He placed them among the Lepidoptera, considering them to be a group of archaic Heterocera which arose in the Jurassic and died out without leaving any descendants. This interpretation has been challenged by Rebel, and then by Martynov, who demonstrated that what Handlirsch took for scales on the wings of the PALAEONTINIDAE were only coloured tubercles like those of the MESOGEREONIDAE, and of certain living cicadas. We can no longer doubt today that the PALAEONTINIDAE are really Homoptera, close to the MESOGEREONIDAE.

The ancestors of the PALAEONTINIDAE must have divided off from the Gondwanian stock of the MESOGEREONIDAE at the end of the Palaeozoic, and migrated into the Northern Hemisphere. Of two genera described by

Martynov from the Lower Lias of Ferghana, *Palaeontinodes* and *Palaeontinopsis*, the former established a clear transition between the *Mesogereon* of Ipswich and the PALAEONTINIDAE of the European Jurassic (*Palaeontina*, *Limacodites*), described by Handlirsch.

The PALAEONTINIDAE disappeared at the end of the Jurassic. Example:

Eocicada microcephala Opp., from the Upper Jurassic of Bavaria. Pl. 3, XIII (D).

The Sternorrhyncha

The PSYLLIDAE and APHIDIDAE are known as fossils from Tertiary deposits, mainly from the Baltic Amber. In spite of the lack of any earlier evidence, it cannot be doubted that these Homoptera derive directly from the Palaeorrhyncha. It has been suggested that the PERMOPSYLLIDAE, from the Lower Permian of Kansas, may be the ancestors of all the Sternorrhyncha.

40. Order **Heteroptera**. The earliest Heteroptera, without doubt arisen from a Homopteron stock, were found in the Upper Trias of Ipswich. These are the DUNSTANIIDAE, Gymnocerata on the line of the PENTATOMIDAE, and the TRIASSOCORISIDAE, Cryptocerata that seem to be the ancestors of the NOTONECTIDAE. The Liassic deposits of the Ferghana have not yielded any Heteroptera, but these turn up in numbers in Western Europe, from the Upper Lias onwards.

A whole series of families have been described by Handlirsch from the remains of Heteroptera from the Upper Lias of Mecklenburg: these are hardly recognizable, but are more or less reminiscent of the PENTATOMIDAE and the LYGAEIDAE. In more recent deposits, among the lithographic stones of Solenhofen, are to be found well-preserved imprints which show that by the Upper Jurassic all the types of the Cryptocerata, NEPIDAE, BELOSTOMIDAE, CORIXIDAE, NAUCORIDAE, and NOTONECTIDAE, were differentiated. Examples:

Mesonepa minor Handl., from the Upper Jurassic of Bavaria. Pl. 3, XIII (E).

Mesobelostoma deperditum Germ., from the Upper Jurassic of Bavaria. Pl. 3, XIII (F).

In the Tertiary, nearly all the living families of Heteroptera are represented either by living genera, or by other closely related. Examples:

Notonecta harnacki Schlecht., from the Upper Oligocene of Rhenanie. Pl. 3, XIII (G).

Thanasimosphaeria haasei Heer, a Scutellerid from the Upper Miocene of Baden. Pl. 3, XIII (H).

Aradus superstes Germ., an Aradid from the Baltic Amber. Pl. 3, XIII (I).

How the Insects Spread over the Earth

THE earliest known terrestrial arthropods are Silurian scorpions (*Palaeophonus*), which differ little from living forms. To find remains of insects we have to wait until the Devonian, when a tropical flora was well-established in Laurentia. Traces of this occur in Northern Europe and in North America.

The deposits of Gilboa Dam, near New York, contain the remains of forests, with giant Horsetails, Cordaites, Club-mosses and Pteridosperms. This vegetation extended as far as Spitzbergen, and was obviously evolved in a very hot and humid climate. Unfortunately we do not know what insects were to be found among it. In contrast, the great Devonian Peat Moss at Rhynie, in the North of Scotland, has yielded remains of Arachnida and of Insects. As we have seen, the latter were Collembola.

It is interesting to observe that the most ancient of the insects belong to the Sub-Class Collembola, which is the most primitive and surely belongs as much to the Myriapoda as to the Insecta. Moreover, these Devonian Collembola were nearly as highly evolved as those of the present day. We must therefore conclude that their stock must have existed millions of years already when we find it in the peat mosses of Rhynie.

The existence of Devonian Collembola is also significant proof that the Apterygota are not degenerate Pterygota, as Handlirsch thought they were. Wingless insects came earlier than forms with wings, which do not appear in the fossil-bearing strata earlier than the Carboniferous.

THE FIRST PTERYGOTE INSECTS

The remains of winged insects are not found until 80 million years later, in the coal-measures of the Middle Carboniferous. What is more, they appear there suddenly, in great numbers, very diversified, and in different areas of Laurentia at the same time. Their sudden expansion is no surprise; it is one of the most often quoted examples of the abrupt appearance of a 'cryptogenous' group.

This fauna of Pterygote insects, making its appearance thus in the Laurentia of the Middle Carboniferous, is a fauna appropriate to a hot and humid climate, and its remains are preserved only in the beds of coal formed in zones of equatorial rain forest. Now the coal measures do not

begin until the Middle Carboniferous, the Lower Carboniferous being represented only by marine sediments, both in Western Europe and in North America.

On the other hand, when we consider that 60 million years elapsed between the beginning and the end of the Carboniferous, we must assume that during this enormous lapse of time, three times as long as the whole of the Tertiary, the fauna and flora must have undergone various movements in correlation with the climatic changes during the period. It is impossible to say where the insect stocks came from that suddenly arose during the equatorial period in the Carboniferous in Laurentia: but if, as the geologists suppose, the North Pole in Devonian times was right in the middle of the Pacific Ocean, the Tropics of that time must have extended over what are now the Polar Regions. This must have been so in Greenland and Baffin Land, for there to be fossils there of the true ancestors of the Laurentian Pterygota of the Carboniferous.

THE SUCCESSION OF FAUNAS AMONG THE INSECTS

During the Carboniferous and Permian, therefore, many lines of primitive insects evolved in the equatorial belt of Laurentia, which corresponds to Eastern North America and Western Europe in present-day geography. These were Palaeoptera and Polyneoptera, all hemimetabolous, the Devonian ancestors of which had probably come from more northerly regions.

During the same period a fauna adapted to a temperate or cold climate developed in Gondwanaland mainly composed of Paraneoptera (Homoptera) and Oligoneoptera. In this fauna are to be found the stems of all the groups of Holometabola, that is of those insects that have a complete metamorphosis, with a quiescent pupal stage. Holometabolism, like homeothermy in the higher vertebrates, is an adaptation that arose under the influence of a temperate climate, with its cold winters.

It is probable that this primitive Gondwanian fauna came into being in the temperate regions of the great asylum that was then Gondwanaland. It is known to us, however, only from the sub-polar deposits of Eastern Australia, and through the migrations of some of its members across the Tethys into Laurentia, into Kansas on the one hand and into Russia on the other.

At the end of the Permian Laurentia became colder, passing into a sub-tropical climate, and becoming arid; Gondwanaland, on the other hand, became warmer, so that the climates of the two great asylums became more alike. Considerable interchanges of fauna then took place, encouraged by temporary recessions of the Tethys Sea. The majority of the primitive lines that had appeared in the hot and humid forests of Laurentia became extinct, with only a few groups, such as the cockroaches, managing

to survive and eventually to spread all over the earth. At the same time the Gondwanian groups spread into Laurentia and Angara Land. The first Holometabola arrived with the Conifers, the primitive Reptiles and the ancestral stocks of the Mammals.

Thus, at the end of the Palaeozoic the Insect fauna of the whole world consisted of a mixture of lines of very different origin, some Laurentian and some Gondwanian. During the Mesozoic the evolution of these groups was modified by the fragmentation of Gondwanaland, and the consequent isolation of populations of insects.

All this story of the evolution of the Insects during the Palaeozoic rests upon a mass of palaeontological evidence that has accumulated in recent years. When we come to the Mesozoic we have to rely more on biogeographical evidence to reconstruct the history of the various lines of insects. The history of living groups, which often goes back to the Trias, and a study of the phylogeny of their genera and families are often as illuminating as the study of the fossil forms alone. This combination of historical biogeography with palaeontology enables us to follow the evolution and dispersion of the insects without a break, with the famous Upper Triassic deposits of Ipswich, Queensland, acting as a link between the Palaeontological data relating to the Palaeozoic and the biogeographic data of the Mesozoic and the Tertiary.

The lines of evolution that it is possible to trace in this way can be arranged in a certain number of categories, each with its own origin, and these again can be sorted into *Laurentian*, *Gondwanian* and *Angaran* lines. It has been necessary to recognize a distinct Angaran fauna, derived from immigrants from eastern Gondwanaland. These Angaran lines spread along with the first Angiosperms from the Middle Cretaceous onwards, and during the Tertiary covered the whole Northern Hemisphere.

Thus, the history of the Laurentian and Gondwanian lines began back in the Palaeozoic, but that of the Angaran lines does not start until the Cretaceous. The evolution of the first two faunas took place on a world stage; that of the Angaran fauna is confined to the two northern continents, remnants of Laurentia and Angara Land, which can be jointly known as '*Laurasia*', and which nearly correspond to the Holarctic Region of the biogeographers.

A. The Laurentian Fauna of the Palaeozoic

In the area that we are referring to as Laurentia two very different faunas followed each other during the Carboniferous and the Permian.

THE CARBONIFEROUS FAUNA. During the Middle and Upper Carboniferous, when Eastern America and Western Europe were in a tropical rain-belt, a rich and varied fauna populated the forests. The insects included two of the most primitive groups of Pterygota, the Palaeoptera

and the Polyneoptera, in about equal numbers. All the evidence points to the fact that these two great groups came into being in Laurentia, and that at first they were the only insects present there.

It was in this period that there flourished the Eupalaeodictyoptera, the Megasecoptera, with their giant forms (Pl. 3, V), the Protephemeroptera (*Triplosoba*), quite a number of archaic families of cockroaches, the Protoblattoptera, the Protorthoptera, and finally the Orthoptera Saltatoria (*Oedischia*).

All these insects were very primitive; they had the same general plan as the living forms, it is true, but were very little evolved in comparison. Their organs, hardly specialized, were homodynamic; that is, the various pairs were similar to one another, each pair consisting of segments that were nearly alike. The three pairs of legs were identical; the two pairs of wings hardly different. The abdomen of the Palaeoptera consisted of 11 segments, of which the first 10, all alike, bore paranotal lobes, comparable to the wing-pads of the thorax. The mouthparts were of the chewing type, rarely specialized, and there were 3 ocelli. The insects of the Carboniferous differed from modern insects in the absence of all the complications of shape and form, the reduction and loss of structures, that come about during the specialization of organs. By modern standards they were larvae, or nymphs, with wings.

These primitive Pterygota were relatively very big. The Eupalaeodictyoptera were nearly all huge insects, bulky and heavy, with a wing-span of several inches.

All of them were hemimetabolous, the young forms differing from the mature ones only in not having wings. Almost all—if not all—passed their early stages in water in marshy areas, and in the adult state lived on the vegetation, some being phytophagous and others carnivorous.

This entire fauna, which reached its peak in the deposits of Mazon Creek and Comentry, in the Stephanian Period, became extinct by stages during the Permian, as the hot climate gradually gave place to cooler and more arid conditions.

THE PERMIAN FAUNA. At the time that the Carboniferous lines disappeared, either by extinction or by migration, other lines gradually arose. These new-comers were probably of the same origin as those they replaced, but they seem to have come in from other areas. Moreover, they were able to spread eastwards in Laurentia because the retreat of the sea from Eastern Europe gave them access to the immense Russian platform right up to the Ural Seas.

These Palaeoptera and Polyneoptera, replacing the Carboniferous forms, were not the only insects of Permian Laurentia. They were reinforced with Gondwanian stocks, which circumvented the Tethys at both ends, invading Laurentia in America and in Russia. A mixture of the two

faunas is to be found in the Deposits of Kansas on the one hand and of Kazan and Archangel on the other. We shall come back to the immigrant stocks later. As for the indigenous Permian stocks, these are still Palaeoptera and Polyneoptera, but different from the Carboniferous groups.

The Eupalaeodictyoptera disappeared suddenly. The Megasecoptera gave place, both in Kansas and in Russia, to other carnivores that were more highly evolved, the Protohymenoptera. In Central Europe were the Protohemiptera (*Eugereon*), sucking the sap of plants. The giant Meganeura were replaced by smaller Meganisoptera (*Typus*), alongside which flew the first dragonflies (Permodonata), migrated from Gondwanaland. The cockroaches, even, belonged to new groups.

All these Permian lines in Laurentia were descended from stems which had evolved in other areas, outside the equatorial zone of the Carboniferous, but so far we have not found traces in any deposits that would tell us where they came from. They are all more specialized than the Carboniferous stocks, and they seem also to have been less numerous.

The majority of these became extinct, in their turn, at the end of the Permian, or during the onset of the Mesozoic. The Meganisoptera, Permoplectoptera and Protoperlaria persisted until the Lias, but all the Permian cockroaches of Laurentia gave way before the invasion of Gondwanian forms.

B. The Primitive Gondwanian Forms

A few groups of Palaeoptera and Polyneoptera seem to have arisen in Gondwanaland, no doubt from Laurentian stocks that had migrated there during the Devonian or the Carboniferous. This is probably the case with the true Ephemeroptera and the Permodonata. The bulk of the Gondwanian fauna, however, is made up of primitive Paraneoptera and Oligoneoptera.

Remains of members of these groups abound in the Permian deposits of Australia, Kansas and Russia. The Homoptera that are found there at first are archaic types, and soon become so numerous that they are more than half the numbers of insects found in these deposits. Along with them appear the first Holometabola, Mecoptera, Planipennia and Coleoptera.

The oldest fossil-bearing deposit known is that of Elmo in Kansas (Lower Permian). The Australian beds at Belmont and Newcastle in New South Wales are more recent, being of the same age as the Russian beds of the Upper Permian. It is a fact that we still have not found any Carboniferous or early Permian deposits in Gondwanaland that would tell us the origin of this fauna, but the distribution of the three groups of fossil-bearing deposits that have been explored suggest that we must look for the ancestral group in some part of Gondwanaland that had a temperate climate during the later Carboniferous, perhaps in Southern

Africa. The Sub-polar deposits of Belmont and Newcastle, like those of Kansas and Russia, show us only emigrant faunas, but faunas whose origin cannot be other than Gondwanian.

In these beds we find that the Paramecoptera of Australia were in the line of descent of the Diptera and Trichoptera, which afterwards spread throughout the world. Among Planipennia, the PERMOCHORISTIDAE, known from Australia and Russia, indirectly gave rise to the PANORPIDAE and BITTACIDAE. The whole Order Planipennia arose in Gondwanaland,

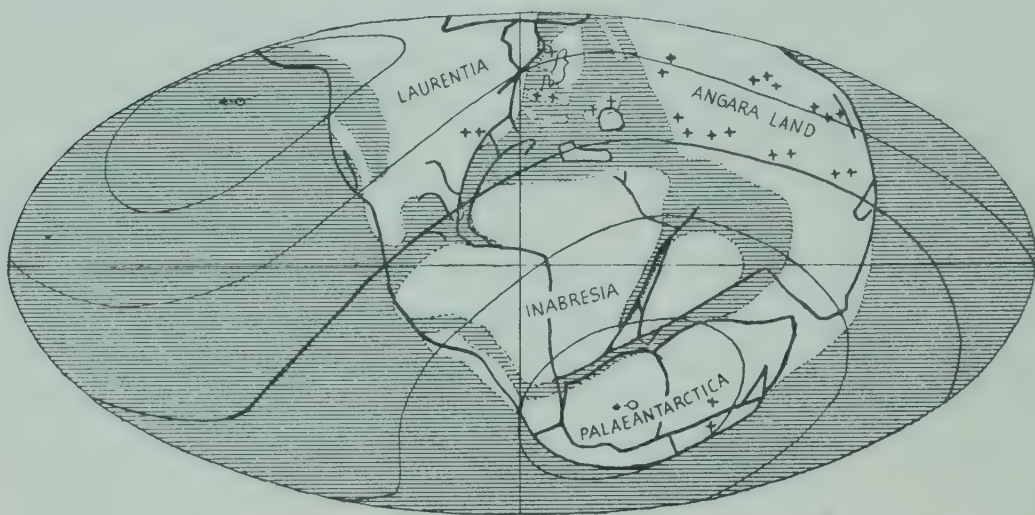


Fig. 139 – The continents of the Upper Jurassic Period, showing the separation of Palaeantarctica from Inabresia by the first splitting of Gondwanaland (grouping of the present continental masses according to KOPPEN and WEGENER).

and we have already mentioned that in Australia the direct descendants of some of these Permian insects are still living in the same places where they occur as fossils.

The Coleoptera also appear in Gondwanaland in the Permian, and CUPEDIDAE are now known from the Lower Permian of Russia (*Tshekardocoleus*).

C. Gondwanaland in the Mesozoic

The descendants of the primitive Gondwanian fauna are widely distributed over the whole world, mingling with several survivors from Laurentian lines, but their Mesozoic evolution took place above all on the fragments of Gondwanaland.

The relative uniformity of the climate, which little by little became sub-tropical on all the continental areas at the end of the Permian, caused the Paraneoptera and Oligoneoptera to be widely dispersed. In the same period the great majority of the Laurentian groups became extinct. Only the cockroaches continued to swarm everywhere, showing that the group

must have a tremendous vitality; its origins go back to the Devonian, 450 million years ago, and it is still thriving today.

Among the Gondwanian groups whose roots are known in the Permian deposits, there are some that became extinct during the Mesozoic, after having swarmed over all the earth. They are known from imprints that have been left in Asia and in Europe. We have seen how in the Jurassic, when the Lepidoptera had not yet come into being, their part was played by Planipennia such as the KALLIGRAMMATIDAE, and Homoptera such as the PALAEONTINIDAE.

When we are dealing with the Gondwanian lines that have survived till the present day, we get better results from methodical study of their phylogeny than from confining our attention to the fossils. By the method of 'biogeography' we can follow their evolution on all the various fragments of Gondwanaland, and we have shown in an earlier work¹ that the lines of evolution fall into three very different types: Palaeantarctic, Africano-Brazilian, and East-Gondwanian.

THE PALAEANTARCTIC GROUPS. The great mass of primitive Gondwanaland began to break up in the Trias, and soon separated into two continents, Inabresia and Palaeantarctica, separated by a primary fissure that gave rise to the Indian and South Atlantic Oceans. South America,

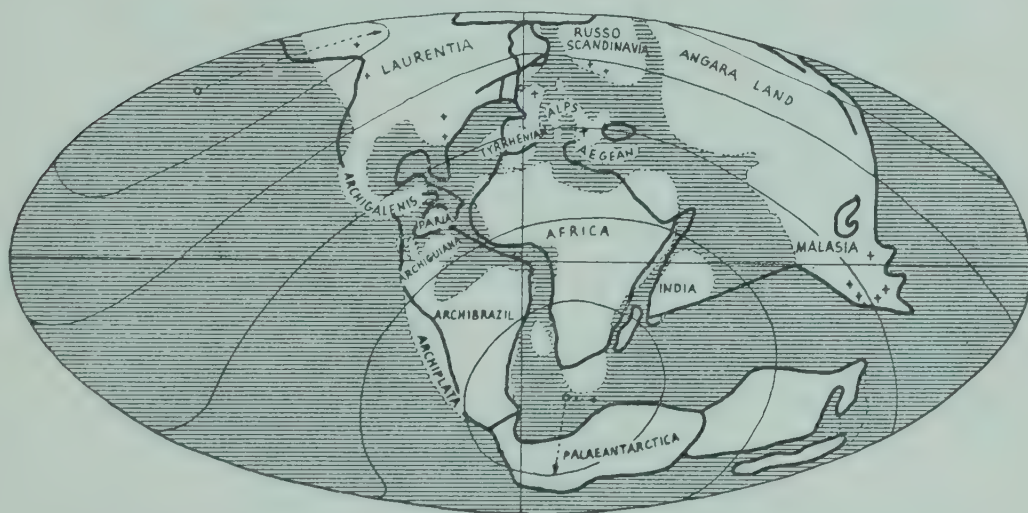


Fig 140 - The continents at the end of the Cretaceous, showing the fragmentation of Inabresia after the opening up of the South Atlantic (grouping of the present continental masses according to KOPPEN and WEGENER).

Antarctica and the Australasian mass remained as one for a long time, forming Palaeantarctica (Figs. 139 and 140).

The South Pole always occupied the centre of Palaeantarctica, so that this continent nearly always had its margins in high latitudes, and

¹ JEANNEL, R. *La genèse des faunes terrestres*. Presses Universitaires de France, Paris, 1942.

communication between one side and another was difficult. All the Palaeantarctic groups were cold-climate forms.

Some spread along the Atlantic shores, from Australia to America, or vice versa. Occasionally they appear in South Africa, like the LUCANIDAE of the genus *Chiasognathus* to which we have referred earlier. Their distribution is comparable with that of a fossil Pteridosperm of the Lower Jurassic, *Thinnfeldia odontopteroides*.



Fig. 141 – Distribution at the present time of an Africano-Brazilian group: the *Hiletidae* Coleoptera; Carabidae). 1: genus *Neohiletus* JEANN.; 2, 3 and 4: genus *Hiletus* SCHIODTE, represented by three sub-genera.

Other Palaeantarctic groups, like that of the MIGADOPIDAE (Coleoptera) spread along the Pacific shores. These are not found in Africa, but survivors occupy South America, Australia and New Zealand. They are younger, since they go with the *Nothofagus* flora, which reached New Zealand in the Upper Cretaceous when the south of New Zealand, though united with Antarctica, had already become separated from Australia.

This Palaeantarctic fauna, adapted to a temperate or cold climate, was able to spread into the Northern Hemisphere, no doubt by way of the Americas. The majority of these northerly migrants became extinct during the Tertiary, but some, such as *Chiasognathus* and *Triplectides* have left traces in the Baltic Amber.

INABRESIA. Facing Palaeantarctica was Inabresia (Jeannel, 1942), an ancient land-mass that today is represented by fragments: Brazil, Africa, Madagascar and India. While Palaeantarctica, with the South Pole in the middle of it, was a reservoir of groups adapted to temperate conditions, Inabresia in the Mesozoic had the fauna of a hot country, and was the source of the groups that fill the tropical regions today.

The insect-fauna was concentrated in the northern part of that great continent, which in Jurassic times stretched for thousands of miles below

latitude 30° S. In this vast area there were two main centres of evolution: in the west arose Africano-Brazilian lines; in the east those of Eastern Gondwanaland.

THE AFRICANO-BRAZILIAN LINES. Many groups of insects can be found in which some species occur in the Brazilian massif, and others of the same group in tropical or southern Africa (Fig. 141). They originated in the western part of Inabresia, before the influx of the Atlantic Ocean, which dates from the Upper Cretaceous. The primitive area thus appears split into two, and since this split has now existed for a long time we find that different genera have been evolved on opposite sides of the ocean.

The Africano-Brazilian stocks spread secondarily into North America at the beginning of the Tertiary, but they did not occupy the whole of South America until after the Oligocene, when that continent took shape. In the Montian, African groups pushed across to India, and they reached Madagascar in the same period, and again in the Pontian.

THE EASTERN GONDWANIAN STOCKS. I give this name to very many evolutionary lines of the present-day fauna of East Africa, Madagascar, India and Malaya, as well as to some in Australia, that are descended from stem-groups peculiar to the eastern part of Inabresia (Fig. 142). The fact that they extend into Australia enables us to determine their age.



Fig. 142 – Distribution at the present time of an Eastern Gondwanian group: the genus *Perileptus* (Coleoptera; Carabidae). The original area of distribution was round the periphery of the Indian Ocean; the arrows indicate the migration of certain species at the beginning of the Tertiary (Montian).

The oldest of them, going back to pre-Jurassic times, occupy the whole of Australia and New Zealand. Thus they must have been dispersed before the separation of Australia from the Indo-Malayan land-mass, that is to say, before the Upper Jurassic. These are the 'pre-Jurassic lines'.

Other lines, the 'post-Jurassic lines', no doubt originated in Indo-Malaya, and have spread freely into Africa and Madagascar, but were

not able to reach Australia until the Pleistocene, when there was a temporary land-bridge between Malaya and New Guinea. These post-Jurassic lines did not penetrate farther than Queensland, and are completely absent from New Caledonia, New Zealand and Tasmania.

A remarkable fact about the Eastern Gondwanian stocks is that they spread through the Northern Hemisphere in the Montian. On the one hand, Indo-Malayan species populated China and Japan; on the other hand, many groups crossed the Mediterranean by way of the Aegean, and so to all the Mediterranean Basin. In this way many of them colonized Southern Europe as far as the Canaries, and some reached North America when the warm climate of the early Tertiary allowed them to spread by way of Northern Europe and Greenland. There are some that at the present day survive only in the Antilles and the Mediterranean.

D. The Tertiary Fauna of Angara Land

Angara Land was a land-mass in which the climate remained relatively constant, and it was populated during the Mesozoic by groups of insects coming from Eastern Gondwanaland. We can look upon it as an asylum in which were perfected the stem-groups of a great many lines that colonized the entire Northern Hemisphere (Laurasia) during the Tertiary.

The migrations of these Angaran groups towards Europe began in the Middle Cretaceous, and accompanied the first Angiosperms, that is the first plants to have flowers and deciduous foliage. This new flora, which no doubt also came from Angara Land, provided the insects with openings for many new kinds of specialization. Whole groups of insects came into being in association with the flowers and fruit. (Lepidoptera, Diptera, Hymenoptera—both honey-loving and predatory—and flower-living beetles). On the other hand, the accumulation of dead leaves in the forests provided a medium for the feeding of saprophytic forms, and acted as a nursery for the development of internal parasites and cave-dwellers.

THE ANGARAN STOCKS. It was above all in the Montian, when the meridional Ural Sea was dried up, that the Angaran stocks were able to spread towards Europe. All the biogeographers agree that in the Montian important migrations of animals took place eastwards from Central Asia to North America, by way of the Northern Pacific, but it is not very likely that the insects were able to follow this route. While it is true that an isthmus crossed the Northern Pacific in this period, the North Pole at that time lay south of the Aleutian Islands, and a land-bridge in this region would not be suitable as a migration route. The faunal exchanges between Asia and America can have taken place only by way of a 'trans-Arctic route', perhaps directly between the Archipelago of New Siberia, and the basin of the Mackenzie River; that is to say, across what is the Pole

at the present day, assuming that the Arctic Ocean had still not opened up. But, in fact, most of the Angaran stocks spread about the Northern Hemisphere by way of Europe.

THE COLONIZATION OF EUROPE. Throughout the Mesozoic Period, Central and Southern Europe were inundated by the sea. Great islands, remnants of the Hercynian chains of mountains, were left surrounded by the sea. Mesozoic Europe had nothing of the character of an asylum, but was occupied by an immigrant fauna.

The continental period in Europe begins in the Montian, when the seas retreated from Eastern Russia, and the barrier that had separated Angara Land from Europe existed no longer. During the five million years of the Montian Period, the European fauna was reinforced freely round both the north and the south of the vast Aralo-Caspian Basin which existed as an extension of the Black Sea.

After the Montian, and throughout the Eocene, the sea returned to Central Europe, which once again became an archipelago. The spread of an inlet of the sea across the Obi region of Western Siberia united the Arctic and Mediterranean Seas, and once again cut off migration from Angara Land. But from the end of the Oligocene, the drying up of the Obi Sea released these migrants again to a Europe that had certainly become continental again.

COLONIZATION OF THE MEDITERRANEAN. In the Montian, the Angaran stocks which came round the northern end of the Aralo-Caspian Sea spread into the Mediterranean Basin via a series of wooded mountain ranges, from the Caucasus to the Pyrenees (Fig. 143). This area (the *Mésogéide* of Jeannel) was split into two in the Lutetian by the incursion of the sea over the Italian Peninsula, and it is from this period onwards that the Mediterranean fauna has evolved in two parts: a Western Mediterranean (Tyrrhenian) fauna and an Eastern Mediterranean (Aegean) one.

On the other hand, the Angaran stocks that passed to the south of the Aralo-Caspian Sea came into the Southern Aegean Region (Fig. 144), and were trapped there by the waters of the Transaegean Rift (Jeannel, 1923). This long marine trough united the Mediterranean with the Aralo-Caspian, and thus split the Aegean land-mass into two parts from the Cretaceous until the Upper Miocene (Tortonian). It played a major role in the colonization of the Mediterranean, because it was not until the end of the Tortonian, in the Pontian, that the groups imprisoned in the Southern Aegean Region could escape towards Western Europe.

Mixed with these Angaran stocks were some of Eastern Gondwanian origin as we have already seen, and both spread westwards right up to the lands bordering on the Atlantic. The isolation of the Canaries and of Madeira dates from the Burdigalian inundation (Middle Miocene), while

the Cape Verde Islands without a doubt were attached to Africa for a longer period. As for the Azores, it seems that European stocks must have had access to them again in the Quaternary.

COLONIZATION OF THE HOLARCTIC REGION. The Angaran groups that reached Europe in the Montian occupied the ancient massifs (the

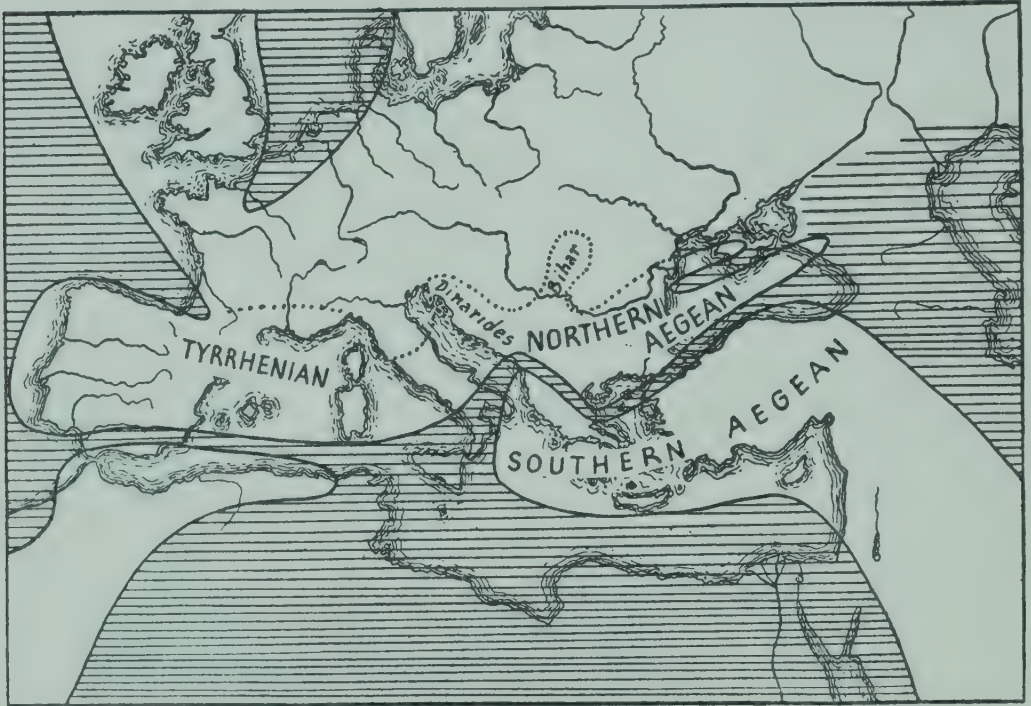


Fig. 143 – A diagrammatic picture of the Mesogeal Area of the early Tertiary. To the north it is bounded by the geosyncline of the Alps (dotted line), to the south by the Mediterranean. The Transaegian Rift cuts in two the ancient Aegian massif, leaving a southern mass which was linked with Gondwanaland during the Montian.

Bohemian, the Ibero-Mauritanian, and the Central Massif of France), which had remained isolated as big islands in the middle of the Lutetian seas. They also reached the Hercynian massif of the Appalachians in North America, by way of the Armorican and Scandinavian massifs and the North Atlantic seaboard. This migration round the North Atlantic was helped by a warm climate similar to that of the Mediterranean at the present day, which prevailed in early Tertiary times as far north as Greenland.

In Europe the Angaran groups produced a variety of types of geographical distribution, according to the time at which the migration took place. The principal types are the following:

The Mountain Groups. The incursion of the sea into Central Europe during the Eocene concentrated the earliest Angaran stocks on to the ancient massifs of Bohemia, of Central France, and of the Mediterranean

(Aegean and Tyrrhenian). Later, in the Miocene, when the chains of the Alpine system had arisen, the younger European mountains were populated by groups that came from the older massifs, which in this respect had played the part of asylums. The montane faunas of Europe were thus based upon ancient Angaran stocks (*Nebria*, *Trechus*, etc.).

Arctic Groups. The ancient Angaran immigrants also spread over Northern Europe (the Scandinavian massif, and the Armorican massif) and the north of North America, taking advantage of a warmer climate than that of the present day. These lines persist in the Arctic Zone (*Pelophila borealis*, *Miscodera arctica*, etc.). Most of these Arctic species are found in the British Isles, including Ireland.

Boreo-Alpine Groups. The species of this group have a widespread continuous distribution in the Arctic Zone, and are also represented by colonies isolated on the mountains of the temperate zone. Most authors



Fig. 144 – A diagrammatic picture of Mediterranean Europe in the Pontian. The drying up of the Transaegæan Rift brought to an end the isolation of the Southern Aegean mass, and allowed its fauna to spread over all the Western Mediterranean.

take them to be species that in the beginning were widely distributed at low altitudes during the ice ages of the Quaternary. The retreat of the Pleistocene glaciers was accompanied by a rise in temperature and a relative dryness that set in motion two streams of migration. One went towards Northern Europe, and occupied the parts of the Arctic that

were freed from ice; the other climbed to the tops of mountains into a climate that was comparable with that of the polar tundra.

The present distribution of *Colias palaeno* (Lepidoptera), and that of *Cymindia vaporariorum* (Coleoptera) (Fig. 145) may well be explained in this way, but there are other boreo-alpine species that are surely much



Fig. 145 – The present Boreo-Alpine distribution of *Cymindis vaporariorum* (Coleoptera; Carabidae).

older than the Glacial Period. *Otiorrhynchus arcticus* (Coleoptera), for example (Fig. 146) only occupied those mountains of temperate Europe that are older than the Alps, and which were the result of pre-Oligocene folding, such as the Tatra Mountains, the Central Massif of France, and the Pyrenees. Its dispersion, therefore dates from the Nummulitic. Thus, there exist ancient boreo-alpine groups, contemporaneous with the montane and Arctic groups that we have listed.

Atlantic Groups. The dispersion of the great Mammals that make up the Afro-Malayan fauna coincided with the liberation of the Southern Aegean Region by the drying up of the Transaegæan Rift, in the Pontian. Many lines of insects followed this migration route, and spread towards Western Europe. They went northwards along the Atlantic coasts, as far as the British Isles, the Faroes, and even the coasts of Norway. The submarine relief of the Continental Shelf outlines exactly the ancient Pontian continent on which these migrations took place.

There are many Atlantic species still existing at the present time.

They are always present on the islands of the Western Mediterranean, and in some places in Central Europe. A good example of this is the Beetle *Leistus fulvibarbis*, shown in Fig. 147.

Hercynian and Armorican Groups. A great many European groups occur all over Central Europe, out to Western Siberia, but never go farther north than latitude 60°, nor farther south than the bases of the Mediterranean peninsulas. The area of distribution narrows towards the west, and generally does not pass beyond the meridian of Paris. A very few such species occur in the south of England, where they are referred to as 'Hercynian'. An example is the Beetle *Nebria livida*, shown in Fig. 148.

These Hercynian groups came from Angara Land, and reached Europe in the Pliocene, at the same time as the Mammals that now have a 'Holarctic' distribution. It is always the species of the steppes that are involved, never those that are inseparably tied to the forests.

Hercynian migrations followed one another over long periods of the



Fig. 146 - The ancient Boreo-Alpine distribution of *Otiorrhynchus arcticus* RIGHT. (Coleoptera; Curculionidae). In Central and Western Europe it occupies only the remains of mountain chains that date back to pre-Oligocene times (Tatra; Massif Central; Prepyrenees).

Pliocene. The older were driven westwards by the younger, always following the same route. As a result, some of the ancient groups are today crowded to the west of the region, but a few isolated colonies remain in Central Europe as relicts to remind us that they were once

part of a Hercynian migration. These species trapped in the west are the 'Armorican' ones (Jeannel, 1942).

Armorican groups are found in England, but not in Ireland. Being older than the Hercynian ones, they arrived in France before the inundation of the Straits of Dover barred the way, as it did to the later ones.



Fig. 147 - An Atlantic type of distribution in the Carabid beetle *Leistus fulvibarbis* DEJ.

Occasionally there are pairs of species very closely allied, one of which is Hercynian and the other Armorican. The genus *Choleva* (Coleoptera) has several such pairs: *angustata* and *cisteloides*; *glauca* and *bicolor*; *fagniezi* and *sturmi*. The first member of each pair is Armorican, and the other is Hercynian. Thus, we are evidently dealing with two successive migrations of the same group (Fig. 149).

Finno-Siberian Groups. The retreat of the Pleistocene glaciers, which made the Arctic countries of Europe habitable, coincided with a final migration of the Angaran groups, which took place in the Quaternary. There are now many species found in the Transbaikal and in Mongolia, identical, or nearly identical with species found in Northern Scandinavia. This is the 'Finno-Siberian' distribution, of which the genus *Catops* (Coleoptera) affords several examples. One thing which distinguishes these species clearly from the Arctic species is that none of them reaches the north of the British Isles.

THE COLONIZATION OF NORTH AMERICA. In North America, the

Angaran stocks which came across the North Atlantic, are mingled, firstly with archaic stocks that remain from the ancient Laurentian fauna, and secondly with South American stocks that reached the Northern Hemisphere in the Montian. Thus elements of Palaeantarctic, Inabresian and Angaran faunas go to make the immensely varied fauna of North America.

Certain of these South American stocks invading North America have even advanced towards Europe by the northern route, thus reversing the track of the Angarans. Many are found in the Baltic Amber, but they have all vanished from the living insect fauna of Europe.

Finally, the emergence from the sea of the Isthmus of Panama in the Pliocene made possible a new and very recent migration from the south. The way has been opened for the tropical 'Sonorian' species, whose presence up to the latitude of New York gives the North American insect fauna an unexpectedly subtropical aspect.



Fig. 148 - A Hercynian type of distribution in the Carabid beetle *Nebria livida* L. The crosses indicate isolated localities in England.

THE NATURAL REGIONS OF THE WORLD

The short account that we have just given has followed the vicissitudes of the insects during their colonization of the earth, from the Palaeozoic fossils, through all the geological periods. It may be worth while to complete this essay in 'historic biogeography' (Geonemy) with an account of

the natural regions as they are defined by the study of 'statistical biogeography'.

The distribution of the terrestrial animals of the present day has led to a division of the globe into natural regions, which were defined for the first time by Sclater and Wallace. These authors, and all their successors until now, have taken the Mammals as their raw material, but this choice can be criticized on two grounds. Firstly that the Mammals are warm-blooded (homeothermic), and this makes them far too independent of the external climate to be a good indicator group; and secondly that as a group they are far too young. Moreover, the zoological regions as defined by Wallace are only statistical units, and are not closely related to the evolution of the insect faunas.

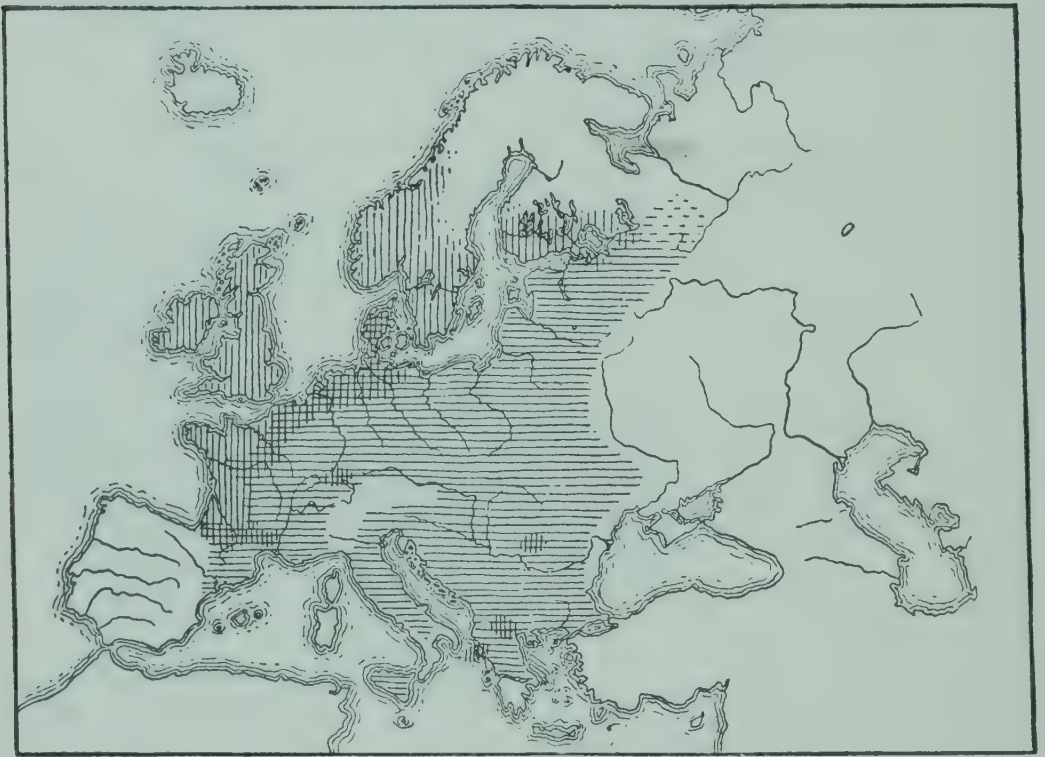


Fig. 149 - Distribution of two *Choleva* (Coleoptera; Catopidae), which form a 'pair' of species: *Ch. angustata* F., an American type (vertical lines), and *Ch. cisteloides* FROL., a Hercynian type (horizontal lines).

As they are accepted today, Wallace's natural regions are five in number. (See Fig. 150.)

Australian Region, where the only endemic Mammals are the Marsupials and the Monotremes. The *Hawaiian Region* has no endemic Mammals, but its fauna is clearly linked with the Australian Region.

Neotropical Region, or South American, has Marsupials, Edentates, and Monkeys with prehensile tails, but no Lemurs.

Ethiopian Region, with Edentates, Lemurs, Primates and Elephants.

The *Malagasian Region* is often separated off, and is characterized by the abundance of Lemurs and the absence of large Mammals.

Oriental Region, or Indo-Malayan, hardly separable from the preceding.

Holarctic Region, with no Primates, no Edentates, no Marsupials, no Elephants.

Holdhaus (1928) has given a good account of the entomological faunas of these five 'natural regions', and shown that they are really heterogeneous mixtures of insects the assembly of which has been brought about by a variety of factors. Their presence in a given region depends on the palaeogeographical history of the continents, the opportunities for dispersion, and conditions of environment, vegetation, and climate, all of which have changed in the course of time. The statistical study of the insect faunas of Wallace's natural regions has little significance. We shall show in the remaining pages that each of these regions is only an area where certain palaeogeographical and ecological conditions are most frequently encountered.

THE AUSTRALIAN REGION

Under this name are united Australia, New Guinea, New Zealand, Melanesia and Polynesia; and the Hawaiian Islands are linked, though for certain groups they have to be considered as an independent area. The area is divided into two Sub-Regions, but these are characterized only by the different way in which they were colonized. The accidents of inter-continental links explains the differences between the faunas of the Australian, Papuan and New Zealand Sub-Regions, and the extreme endemism of the Hawaiian Sub-Region, so far as insects are concerned, merely expresses the isolation of these islands, which goes back to the Cretaceous.

In reality, the essential character of the Australian fauna lies in the fact that it is composed of ancient Palaeantarctic and Eastern Gondwanian stocks, but most of these extend outside the region. The Weber-Wallace line, which passes between Borneo and Celebes, through the Macassar Strait and between Bali and Lombok, is not a true regional frontier, but a no-man's-land in which, in the Pleistocene, an exchange of faunas took place between the Australian Region and the Malayan area. Malayan species invaded northern Australia, while Australian species reached Malaya.

THE NEOTROPICAL REGION

From a faunistic point of view this is perhaps the most clearly defined, but it is certainly the least natural of Wallace's 'natural regions'. The present continent of South America took shape only in the Oligocene, through the merging of three continental areas that had formerly been



Fig. 150 - A MAP OF THE NATU

REGION	SUB-REGIONS
Holarctic	1. Nearctic
	2. Sonoran
	3. European
	4. Siberian
	5. Mediterranean
	6. Central-Asian
	7. Palearctic

REGION	SUB-REGIONS
Neotropical	1. Chilean
	2. Magellanic
	3. Brazilian
	4. Pampean
	5. Mexicano-Andean
	6. Antillean



REGIONS OF THE WORLD.

REGION	SUB-REGIONS
Ethiopian	1. Sudanese
	2. West African
	3. East African
	4. South African
	5. Malagasian

REGION	SUB-REGIONS
Oriental	1. Indian
	2. Indo-Chinese
	3. Malaysian
	4. Philippine

REGION	SUB-REGIONS
Australian	1. Australian
	2. Papuan
	3. New Zealand
	4. Polynesian

separate: *Archiplata* (Chile + Patagonia); *Archibrasil* (the Brazilian massif); and *Archiguiana*. The faunas of these three continental areas had very different origins.

Archiplata was the American extremity of Palaeantarctica, and was the source of all the South American groups of the present day that are remarkable for their affinities with Australia and New Zealand.

Archibrasil was part of Inabresia, and has been a reservoir of tropical groups.

During the Cretaceous and Eocene *Archiplata* extended northwards along the Pacific coast until it met with North America, and in this way Chilean elements entered the insect fauna of the Northern Hemisphere (*Anthobium*, *Erirrhinus*, *Erebia*, *Argynnis*).

It follows from this that the sub-divisions of the Neotropical Region, as they have been defined by the biogeographers, are not all equally valid. The Chilean and Magellanic Sub-Regions are the remains of Palaeantarctica, invaded after the Oligocene by Inabresian stocks. The other Sub-Regions, Brazilian, Pampean, Mexicano-Andean, Antillean, derive from Inabresia, and such differences as exist between them are attributable to climate. Their fauna has, moreover, overflowed widely in the north during the Pleistocene, when the rise of the isthmus of Panama allowed the Sonorian migration to take place.

THE ETHIOPIAN REGION

The basis of the African insect fauna is again a mixture of heterogeneous stocks. They all belonged to Inabresia, and consequently are specialized to tropical life, but the Africa that they inhabit today is only a part of their primitive homeland.

While the Ethiopian Region is quite well defined among the Mammals, this is not at all so for the insects. If there seem to be endemic groups of insects that comes about merely through incomplete systematic knowledge, which has not yet revealed the true affinities of the species. In reality, one part of the Ethiopian fauna is composed of Africano-Brazilian lines, found in South America; the other consists of the many Eastern Gondwanian groups that are found also in the Oriental and Australian Regions.

The West, South and East African Sub-Regions have absolutely no biogeographical validity. The Malagasian Sub-Region is better characterized, and includes Madagascar, the Comoro, Seychelles and Mascarene Islands. But here, too, we find a mixture of stocks, the African mixing with a minority of 'Lemurian' groups, direct from India.

THE ORIENTAL REGION

Even as far as Mammals are concerned, this Region is hardly to be separated from the Ethiopian. Composed of the Asiatic peninsulas to the

south of the Himalayas, and including the archipelagoes to the south of Malaya, this Region, like the Ethiopian, is populated with a mixture of Africano-Brazilian and Eastern Gondwanian stocks. The insect fauna is a very rich one, and this is perhaps the major characteristic of the Region.

The Sub-Regions, Indian, Indo-Chinese, Malayan, and Philippine, are not very distinct, and interchanges have taken place among them during Quaternary times. The first one, the Indian Sub-Region, ranges from Ceylon to the slopes of the Himalayas, and comprises so many different climates that it lacks any unity.

THE HOLARCTIC REGION

All the Regions so far mentioned are therefore artificial ones, and their faunas are no more than mixtures, in various combinations, of stocks that arose during the Mesozoic on the fragments of Gondwanaland. This is no longer true when we come to the Holarctic Region. This Region covers all the temperate and frigid zones of the Northern Hemisphere, while the greater part of the other Regions lies in equatorial and tropical zones.

The Holarctic Region corresponds to 'Laurasia', of which we have spoken earlier, an area formed around the two ancient asylums of Laurentia and Angara Land. Thus the Holarctic Region could be called the 'Laurasian Region', and set in contrast to all the others, which could be grouped together as 'Gondwanian Regions'. The colonization of the Gondwanian Regions was carried out by stocks that came from Gondwanaland, having evolved there in the Mesozoic; the population of Laurasia was a result of Angaran migrations, dating back only to the Tertiary, to which were added from the Montian onwards those Eastern Gondwanian groups that managed to cross the Mediterranean.

The Angaran groups only rarely spread beyond the southern boundary of Laurasia, and they impinge on the Gondwanian Regions at three points only: on the Mexican mountains; on those of Abyssinia and East Africa; and in the Philippines and Formosa.

It is sounder to stop thinking of the Nearctic and Palaearctic as two distinct Regions. The only difference between them is that the North American fauna contains some South American elements that made use of the north-south orientation of the mountain chain.

The Palaearctic Sub-Region has itself been divided into natural provinces, the number of which has been added to by Semenov-Tian-Shanski. Most of these are based on purely statistical data, and do no more than emphasize the multitude of local climates that are to be found in the immense area of Eurasia.

All the same, it is possible to recognize some Sub-Regions in the southern Palaearctic. The *Mediterranean Sub-Region* in Europe, and

Semenov's '*Palaearctic*' *Sub-Region* of South-East Asia correspond on the whole to territories that were reached by particular waves of migration from Eastern Gondwanaland, the one towards the Mediterranean as far as the Atlantic Islands, and the other through Eastern Asia as far as Japan.

As for the 'Central-Asian Sub-Region' of Semenov, which is intercalated between the two preceding ones, this is really no more than a belt of deserts that are an extension of the desert belt of the Sahara, Arabia and Turkestan.

Index

A

- abdomen, 53
 - appendages of, 54
 - segmentation of, 19
- Acerentomonidae, 87
- achrestogonimous termites, 218
- Acridioidea, 100
 - fossil, 285
- Actaletoidea, 87
- active groups of insects, 195
- Aculeata*, 107
- Adenosyne*, 289
- Adiphebiidae, 271
- Aegean fauna, 321
- Aeromyrma sophiae*, 304
- Aeroplanidae, 281
- Aeschna*, mouthparts, 40
- Aeschnidium densum*, 265
- Aeschniopsis*, 265
- Africano-Brazilian lines of evolution, 319
- air-sacs, 62
- alimentary canal, 57
- alutaceous network,
- anal glands, 59
 - veins, 51
- Anamorpha*, 25
- anamorphous development, 53
- Angara Land, 232
 - in Tertiary, 320
- Anisoptera, 98
 - fossil, 265
- Anisozygoptera, 264
- Anoplura, 108
- antennae, 33
 - of carnivorous insects, 163
- Anthiidae, 294
- antiquity of insects, 230
- ant-lions, 102
- ants, social life of, 204
- ant-stables, 207
- Anuridae, 87
- Aphaniptera, 106
 - fossil, 301
- Aphanipteroidea, 239
- Aphthoroblattina johnsoni*, 266
- Apithanidae, 278
- apodemes, 28
- apodous larvae, 80
- aposematic coloration, 177
- aquatic insects, respiration of, 126
- Aradus superstes*, from amber, 310
- archedictyon, 242
- Archegetes*, 295
- Archelytridae, 287
- Archeptyllidae, 305
- Archescytina permiana*, 308
- Archibrasil, 332
- Archicoleoptera, 288
- Archiguiana, 332
- Archimastax americanus*, 278
- Archimylacridae, 266
- Archipanorpidae, 298
- Archiplata, 332
- Archisialidae, 294
- Archisoptera, 274
- Archithemidae, 264
- Archodonata, 255
- Archostemata, 289
- Archotypus*, 258
- Arctic groups of insects, 323
- Arctocoleus*, 287
- Arixenia*, 101
- Armorican groups of insects, 325
- arolium, 47
- Arrhaphipterus*, 289
- Arthropleona, 87
- Arthropoda, 19
- Ascalaphus, 297
- assemblies of insects, 193
- Asthenohymenidae, 255
- 'asylums', 232
- Asyncritidae, 271
- Atelura formicaria*, 212
- Atlantic groups of insects, 324
- attack, means of, 162
- Auchenorrhyncha, 108
 - fossil, 308
- Australian Region, 328
- Australo-Oriental lines of evolution, 319
- axillary sclerites, 49

B

- bees, dance of the, 189
- behaviour of insects, 159
 - conscious, 183
- Bellicositermes*, 219, 221

Belmontia mitchelli, 298
 Berothidae, 295
 biocenoses, 198
 Bittacidae, 103, 298
Bittacus, mouthparts of, 39
 blastoderm, 74
 Blattelytridae, 287
 Blattidae, fossil, 265
 Blattopteroidea, 98, 239, 265
 blood, 130
 -gills, 62, 127
 Boreo-Alpine groups, 323
 Brachycera, 106
 brain of insects, 66
 Breyeriidae, 247
 bristles, 30
 Brodiidae, 251
 'Bug-nosed Dragonfly', 230, 250
 bumble-bees, social life of, 202
 Buprestidae, 294

C

Cacurgidae, 278
 Caloneuroidea, 281
Calotermes, 215
Calvertiella, 255
 camouflage, 170
Campodea, 90
 Campodeidae, 241
 campodeiform larvae, 80
 Camptoneuridae, 279
Camptotaxineura, 261
 Campylopteridae, 251
 Canadian Shield, 232
 cantharidin, 130
 Carabidae in termites' nests, 225
 Carboniferous, insects of, 311
 cardiac valve, 58, 118
 cardo, 37
 carnivorous insects, 115
 Cassidinae, 29
 castes, 213
 cellulose, digestion of, 214
 central nervous system, 65
 cerci, 55
 cervical sclerites, 43
 Chaulioditidae, 294
 Cheleutoptera, 100
 chemotropism, 139
Chiastognathus, 294, 318
Choleva, 326
 chordotonal organs, 70
 Chresmodidae, 281, 284
 Chrysopidae, 296
 Cicadopsyllidae, 309
 Cicindelidae, 294
 circulatory system, 62, 130

Cixiidae, 309
 classification of insects, 84
 clethrophagous insects, 114
 click-beetles, action of, 158
 Cnemidolestidae, 278
 coarctate pupa, 81
 cockroaches, Mesozoic, 267
 Palaeozoic, 266
 Coleoptera, 101
 fossil, 288
 Coleopteroidea, 101, 239, 288
 Coleoscytidae, 309
Colias palaeno, 324
 Collembola, 87, 240
 colours, appreciation of, 132
 commensals, 181, 211, 224
 commissures, 66
 compound eyes, 33
 Comstock and Needham system, 51
 concave veins, 51
 conditioned reflexes, 183
 connectives, 66
Conocephalopsis, 285
 conscious behaviour, 183
 convex veins, 51
 coprophagous insects, 115
Coptotermes, 218
 corium, 109
 coronal suture, 32
 Corydaloididae, 251
 costa, 51
 costal margin, 49
 coxa, 44
 crop, 57, 118
 cross-veins, 242
 crowds, 193
 Crustacea, 22
 Cryptocerata, 109
 cryptogenous group in evolution, 311
 ctenidia, 106
Cubitermes, 219
 cubitus, 51
Culex, mouthparts of, 40
 Cupedidae, 290
 Curculionidae, 294
 cutaneous respiration, 127
 cuticle, 27
 Cychritidae, 294
 cychrization, 164
 Cyclorrhapha, 106
Cymindis vaporariorum, 324
Cyrtophyllites rogeri, 285

D

dance of the bees, 189
 death, feigning of, 168
 defensive mechanisms, 164

dermal structures, 29
 Dermaptera, 101
 fossil, 288
 Dermapteroidea, 101, 239, 286
 deutoplasm, 74
 Dichentomidae, 305, 308
 Dictyomyliacridae, 267
 Dictyoneuridae, 246
 Dictyoptera, 98
 fossil, 265
 digestion, 116
 extra-oral, 117
 intestinal, 118
 system of, 57
 digging, by insects, 158
 Diplura, 90
 Diptera, 106
 fossil, 300
Ditaxineura, 261
Doritis bosniaskii, 300
 dorsal vessel, 63
 Doteridae, 257
 drill, 184
 Driver Ants, 205
 Dunstaniidae, 310

E

ectoparasites, 182
 Ectotropha, 90, 241
 egg-bursters, 76
 Elcanidae, 284
 Elmo, Kansas, 315
 Elytroneuridae, 286
 Embioptera, 100
 fossil, 286
 embryonic development, 74
 empodium, 47
 endocuticle, 27
 endoparasites, 182
 Endopterygota, 77
 endoskeleton, 28
 Ensifera, 100
 Entotropha, 90, 241
Eoblatta robusta, 271
Eocicada microcephala, 310
 Eosagrionidae, 264
 Eosotomonidae, 87
 Epallagidae, 264
 Ephemeroptera, 91, 239
 Ephemeropteroidea, 256
Ephialtes jurassicus, 304
 epicranium, 31
 epicuticle, 28
Epideigma elegans, 271
 epimeron, 44
Epimorpha, 26
 epimorphous development, 53

episternum, 44
Erebus agrippina, 27
 eruciform larva, 80
 Ethiopian Region, 328
 Eubleptidae, 247
 Eucaenidae, 271
Eucaenus ovalis, 274
Eugereon, 230, 315
Eugereon böckingi, 91
 Eugereonidae, 250
 Eumegasecoptera, 251
 Eupalaeodictyoptera, 243, 314
 Euplecoptera, 280
 Euplectoptera, 257
 Europe, colonization of by insects, 321
 Eusteniidae, 280
Eutermes, 213
 evertible glands, 166
 evolution of insects, 229
 excretion, 121
 excretory organs, 63
 exocuticle, 27
 Exopterygota, 77
 explosive glands, 165
 exuvium, 76
 eyes, 32, 131
 compound, 33, 68
 simple, 32, 68

F

faecal food, 119
 false legs, 55
 fatbody, 64, 122
 feeding habits, 113
 femur, 45
 Finno-Siberian groups of insects, 326
 flight, 162
 foetometamorphosis, 83
 fore-gut, 57
 Forficulidae, 288
Formica fusca & *F. sanguinea*, 210
 fossorial legs, 47, 160
 frequencies, range of, 135
 frons, 32
 fungus gardens, 220
 funicle, 34

G

Gaesomyrmex corniger, 304
 galea, 37
 ganglia, 65
Geinitzia, 280
 genitalia, 54
 geological periods, table of, 237-9
 Geraridae, 275
Gerarus, 230
 Germanoptera, 280

germ band, 74
 gills, 127
 gizzard, 58
 Glosselytroidea, 281
Glossina oligocena, 301
Glyptus, 225
 Gondwanaland, 232, 312
 gregarious insects, 194
Grylloblatta, 281
 Grylloblattidae, 100
 Gymnocerata, 109
 gynandromorphs, 148
Gyrophlebia longicollis, 275

H

Hadentomoidea, 255
 haemocoele, 63
 hairs, 30
Halter americanus, 297
 halteres, of Diptera, 50
 Haplopteroidea, 278
 harvesting ants, 206
 hatching, 76
 Hawaiian Sub-Region, 328, 329
 head, 31
 hearing, 135
 heart, 63
 hemelytra, 50
 Hemerobiidae, 102
 fossil, 295
 Hemerobiioidea, 295
 Hemimerus, 101
 Hemimetabola, 77
 Hemiptera, 108–9
 mouthparts of, 42
 Hemipteroidea, 108, 239, 308
 Hercynian groups of insects, 325
 hermaphrodites, 71, 143
 Heterometabola, 239
 Heteroptera, 109
 fossil, 310
 hind-gut, 59
 hive-bees, 203
Hodotermes, 213
 Holarctic Region, 333
 insects, origin of, 322
Holocompsa fossilis, 270
 Holometabola, 77, 239
Homaloneura, 247
Homaloneurina, 247
 homing, 186
 Homiopteridae, 247
 Homoptera, 108
 fossil, 308
 honey ants, 207
 Honey Bee, mouthparts of, 39

hygrotropism, 139
 Hymenoptera, 104
 fossil, 301
 Hymenopteroidea, 239
 hypermetamorphosis, 81
 hypodermal layer, 27
 hypognathous head, 32
Hypoperla, 280
 hypopharynx, 38
 humidity, effects on insects, 139

I

Idelididae, 279, 280
 imaginal buds, 81
 imago, 81
 Inabresia, 318
Inocellia erigena, 295
 inquilines, 182
 insects, colours of, 28
 development of, 74
 morphology of, 27
 origin of, 23
 size of, 27
 instar, 76
 integument, 27
 intersex, 71, 148
 Ipswichidae, 309
Ischiana, 281
 Ischnoneuridae, 275
 Isophlebiidae, 264
 Isoptera, 99, 212
 fossil, 274
 Ithonidae, 297

J

Japygidae, 241
Japyx, 90
 jowls, 31
 jugal field of wing, 49
 jumping, 159

K

Kalligrammatidae, 296, 317
Kazanella, 280
 Kennedyidae, 261
 kleptoparasites, 182

L

Labiduromma exsulatum, 288
 labium, 37
 labrum, 38
 labyrinths, 185

- lacinia, 37
 - mobilis*, 36
- Lampyridae, 294
 - mouthparts of, 42
- language of insects, 188
- Lapropholis*, 241
- Laurentia, 232
 - insects of, 313
- larvae, 77
- leaf-butterflies, 173
 - insects, 172
- legs, 44
- Leistus fulvibarbis*, 325
- Lemmatophoridae, 279, 280
- Lepidoptera, 103
 - fossil, 299
 - mouthparts of, 39
- Lepidothrix*, 241
- Lepisma*, 90
 - embryo of, 75
- Lepismatidae, 241
- Liadotypinae, 258
- Liadoxyela praecox*, 304
- light-production, 65
- light, reaction to, 137
- ligula, 38
- limbs, reflex shedding of, 140
- Liomopteridae, 279
- Lithomantidae, 243, 246
- Locustopsidae, 285
- locusts, swarming of, 196
- Lomechusa strumosa*, 212
- Lophioneura ustulata*, 308
- Lucanidae, 294
- luciferin/luciferase, 65
- luminous organs, 65, 122
- Lycaenidae and ants, 210
- Lycocercidae, 243, 246
 - mouthparts of, 39
- Mecopteroidea, 103, 239, 297
- Mecynopteridae, 246
- Mecynostoma*, 250
- Mecynostomites*, 250
- Mediterranean, colonization of by insects, 321
 - Sub-Region, 333
- medius, 46, 51
- Megaloptera, 102
 - fossil, 294
- Meganeura monyi*, 98, 258
- Meganisoptera, 98, 258
- Megaponera foetens*, 226
- Megapsychops illidgei*, 296
- Megaptilidae, 246
- Megasceoptera, 91, 250, 314
- Megatypus*, 258
- Megelytridae, 287
- Meliponinae, 203
- membranes, 28
- Mengea tertiaria*, 304
- menotaxis, 138
- mentum, 37
- Meropeidae, 298
- Mesephemeridae, 257
- Mesobelostoma deperditum*, 310
- Mesoblattinidae, 267
- Mesochrysopa zitteli*, 296
- Mésogéide*, 321
- Mesogereon superbum*, 309
- Mesonemura*, 280
- Mesonepa minor*, 310
- Mesopsychopsis*, 295
- Mesorrhaphidiidae, 295
- Mesotermitidae, 218
- mesothorax, 42
- metabolism, 121
- metamorphosis, 19, 76
- Metatermitidae, 218
- metathorax, 42
- Metoedischia*, 284
- microphagous insects, 114
- microsculpture, 29
- mid-gut, 58
- Migapodidae, 318
- migration, 162, 197
- mimicry, 171, 178
- Mirotermes*, 213
- Mischopteridae, 254
- Miscodera arctica*, 323
- Misthodotidae, 257
- Mixotermitoidea, 278
- mola, 36
- monophagous insects, 113
- Mountain groups of insects, 322
- mouth, 31

M

- Machilidae, 241
- Machilis*, 90
- Mallophaga, 108
- Malpighian tubules, 58, 63, 121
- mandibles, 35
- mantids, fossil, 270
- Mantispidae, 102
- Martynovidae, 294
- mask of dragonfly nymph, 38
- Mastotermitidae, 99
- maternal care, 155
- mating of insects, 151
- maxillae, 37
- maxillary palp, 37
- Mecoptera, 103
 - fossil, 297

mouthparts, 31–32
 licking and sucking, 38
 piercing, 39
Musca domestica, mouthparts of, 40
 mushroom gardens, 206
 mycetomes, 119
 mycetophagous insects, 115
 Mylacridae, 266
 Mymaridae, 27
 Myrmeleon,
 fossil, 297
 Myrmeleonidae, 102
 Myrmeleonoidea, 297
Myrmecophila acervorum, 212
 myrmecophiles, 211

N

Nassonov, glands of, 134
 nasute soldiers, 213
 natural regions of the world, 327, 330–1
 (map)
 neala, 49, 265
Nebria livida, 325
 neck region, 43
 necrophagous insects, 115
 Necrophasmidae, 281
 Necrotaulidae, 299
 Nematocera, 106
 Nemopteridae, 102
 Neodonata, 259, 264
 Neoptera, 86
 neoteny, 83, 213
 Neotropical Region, 328, 329
 nervous system, 65
 Neuroptera,
 fossil, 294
 Neuropteroidea, 102, 239
Nicoletia, 90
Nomaretus, 294
 North America, colonization of by insects,
 326
Notiothauma reedi, 298
Notonecta harnacki, 310
 Notoptera, 100, 281
 notum, 43
 nuptial dances, 154
 nutrition, 113

O

obtect pupae, 81
 occipital foramen, 31
 occiput, 31
 ocelli, 33, 68
 Odonata, 98
 fossil, 259

Odonatoptera, 98, 239, 258
Oedischia, 314
 Oedischidae, 284
 oenocytes, 64
 oesophagus, 57, 118
 Oligoneoptera, 86, 101, 239, 288
 Oligotoma, 286
 ommatidia, 68
 Onychophora, 22
 ootheca, 265
Opter, 261
 Oriental Region, 329
 orientation, 186
 orthognathous head, 32
Orthogonius, 225
 Orthophlebiidae, 298
 Orthoptera, 100
 fossil, 284
 Orthopteroidea, 99, 239, 274
 Orthorrhapha, 106
Otiorrhynchus arcticus, 324
 ovaries, 71
 ovarioles, 71
 oviposition, 154
 ovipositor, 54
 oxygen, transport of, 125

P

Paedephemeridae, 257
 paedogenesis, 83
 pairs of species, 326
 Palaeantarctica, 317
 Palaearchearctic Sub-Region, 334
 Palaeodictyoptera, 91, 239, 241
 Palaeognathus succini, 294
 Palaeohemiptera, 309
 Palæomantidae, 305
 Palaeontinidae, 309, 317
 Palaeophonus, 311
Palaeopsylla klebsiana, 301
 Palaeoptera, 86, 90, 239, 314
 Palaeorrhyncha, 108, 308
 Palingeniopsidae, 257
Palombolus florigenus, 301
 palps, 37
Panorpa, mouthparts of, 39
 Panorpidae, 103
 fossil, 298
 Panorpoidea, 297
Papilio dardanus, forms of, 151
Parabelmontia permiana, 298
 paraglossae, 38
 Paramecoptera, 298, 316
 Paramecynostoma, 250
 parameres, 56
Paramylacris rotunda, 266

- Paraneoptera, 86, 107, 239, 304
 paranotal lobes, 24, 44, 85
 Paraplecoptera, 275
 parasites of ants, 212
 parasitism, 181
Parastylus, 241
pars stridens, 30
 parthenogenesis, 82, 143
 pattern, changes of, 175
 Paussidae, 294
Paussus, antenna of, 35
Pelophila borealis, 323
 penis, 56
 Pereboridae, 309
 pericardial cells, 64
 peripheral nerve-system, 67
 periplasm, 74
 peritrophic membrane, 59, 118
 Perlidae, 100
Permaeschna, 261
Permagrion, 255
 Permanisoptera, 261
 Permarrhaphidae, 289
 Permian, insects of, 314
Permithone belmontensis, 297
Permoberothe, 295
 Permocapniidae, 279, 280
 Permochoristidae, 298, 316
Permocicada integra, 309
Permocrossos elongatus, 289
Permocupes, semenovi, 290
Permocupoides distinctus, 290
 Permodonata, 259, 261, 315
 Permofulgor, 287
 Permolestidae, 261
 Permopallagidae, 261
Permophilus, 289
 Permoplectoptera, 257
 Permopsocoptera, 304
 Permopsyllidae, 310
 Permraphidiidae, 295
 Permosialidae, 294
Permosisyra, 295
 Permosynidae, 289
Permothemis libelluloides, 255
Permotipula, 300
Petanoptera, 297
 pharynx, 57
 phases of locusts, 196
 Phasmida, 27
 Phasmidae, 100
 Phasmoidea, fossil, 281
 Phasmoptera, 281
 Phloeothripsidae, 305
Pholidophlon, 261
 phoresy, 182
 phototaxis, 138
 phototropism, 137
Phthartus rossicus, 257
 Phylliidae, 100
Phylloblatta carbonaria, 266
 physogastry, 225
 phytophagous insects, 114
 piercing organs, 164
 pigmentation, mechanism of, 176
 pigment, formation of, 28
Pincombea mirabilis, 308
 Planipennia, 102
 fossil, 295
 plants, oxygen from submerged, 129
 Platychoristidae, 298
 Plecoptera, 100, 279
 Plectoptera, 91, 256
 plectrum, 30
 pleurites, 44
 Poduridae, 87
 Poles, movements of, 312
 polyembryony, 83
 polymorphism, 213
 Polyneoptera, 98, 86, 239
 polyphagous insects, 113
Polytaxineura, 261
 Poroblattinidae, 267
Præmachilis, 241
 predaceous insects, 115, 163
 prementum, 38
 prepupa, 82
Prestwichia, 106
 primitive characteristics, 229
 process of cuticle, 29
Prodryas persephone, 300
 prognathous head, 32
Progoneura, 261
 Projapygidae, 241
Prolindenia, 264
 propodeum, 106
 Prosbolidae, 308
 Prosepididontidae, 299
 prostheca, 36
Protagrion, 255
 Protanisoptera, 261
 Protaptera, 25
 protective coloration, 171
 resemblance, 175
 Protelytroptera, 101, 286
Protambia permana, 286
 Protentomobryidae, 240
 Protephemeroptera, 91, 256, 314
 Prottereismatidae, 257
 Protermitidae, 215
 prothetely, 83
 prothorax, 42
 Protoblattoptera, 99, 270, 314
Protobrachyceron liasinum, 301

Protocoleidae, 287
 Protodiplatyidae, 286, 288
 Protodiptera, 300
 Protodonata, 255
 Protohemiptera, 91, 250
 Protihymenidae, 255
 Protihymenoptera, 91, 254
 Protomecoptera, 298
 Protomorpha, 25
Protomyrmeleon, 264
 Protoperlaria, 279
Protophasma, 281
 Protophasmidae, 271
 Protorthoptera, 99, 274, 314
 Protozygoptera, 261
 Protura, 19, 87, 241
 proventriculus, 58
Pseudohymen angustipennis, 255
 pseudopupa, 82
Pseudosirex, 304
 Psocoptera, 107
 fossil, 304
 Psocopteroidea, 107
 Psychopsidae, fossil, 296
 pteralia, 49
 pterostigma, 49
 pterothorax, 42
Pterygonea, 90
 Pterygota, 90, 241
 Ptilota, 90
 puncturation, 29
 pupae, 80
 pupal mandibles, 81
 Pupipara, 106
 pygopod, 56, 157
 pyloric sphincter, 59

R

radial sector, 51
 radius, 51
 Raphidoptera, 102, 295
 rectum, 59, 118
 Reculoidea, 278
 reflex bleeding, 63, 130, 166
 immobility, 168
 conditioned, 183
 regeneration of limbs, 169
 remigium, 49
 reproduction, 147
 reproductive organs, 71
 respiration, 62
 respiratory system, 59
 retinacula, 36
Rhyniella, 240
 royal cell, of termites, 220
 royal jelly, of bees, 116

S

saprophagous insects, 113
 sawflies, fossil, 304
Schedorhinotermes, 218
 sclerites, 19, 28
Scolopendrella, 25
 scototaxis, 138
Scutinoblatta, 286
 Scytinopteridea, 309
 secretions, used for defence, 165
Semenoviola, 288
 sensillae, 67
 sense-organs, 67, 131
 setae, 30
 sex-determination, 147
 sexual characteristics, 150
 shedding of limbs, 169
 shelter and camouflage, 170
 shields, defensive, 167
 sight, in insects, 131
 organs of, 68
 silk production, 124
 spinning of, 171
 Siphonaptera, 106
 Sisyridae, 295
 size of insects, 27
 slave-making ants, 210
 smell, organs of, 67
 sense of, 132
 Sminthuridae, 87
 social groups, 194
 life, 191, 200
 societies of insects, 198
 Sojanocoleidae, 289
 soldiers, of termites, 213
 solitary instinct, 191
 'Sonorian' species, 327
 Spanioderidae, 275
 'spectral attitude', 167
 spermatophores, 73
Sphaeropsocus kunowi, 305
 Spilapteridae, 247, 255
 Spiloblattinidae, 266
 spiracles, 59, 60
 squama, 49
 Staphylinidae in ants' nests, 212
 in termites' nests, 224
 static groups, 194
 stemmata, 32, 68
 Stenodictyopteridae, 246
Stenoneura fayoli, 271
Stenoperlidium, 280
 Stenophlebiidae, 264
 stenus, 38
 stereotropism, 146
 Sternorrhyncha, 108
 fossil, 310

Sthenarocera pachytyloides, 275
 Sthenaropodidae, 284
Stilbocrosis, 246
 stipes, 37
 stone-flies, 100
 Strepsiptera, 107
 from amber, 304
 stridulatory organs, 30, 136
 subcosta, 51
 subcoxa, 44
 suture, 28
 swarming of termites, 213
 swimming, 161
 symbionts, 181
 symphiles, 212
 Symphypleona, 87
 Symphyta, 107
 synechthrans, 212
 synoeketes, 212
 sypharopteroidea, 255
Syscioblatta dohrni, 266

T

taenidium, 61
 Taeniopterygidae, 281
 Tarsophlebiidae, 264
 tarsus, 46
 taste, 134
 organs of, 67
 tegmina, 50
 tegula, 49
 temperature, extremes of, 139
 relation of activity to, 139
 tentorium, 32
 terebra, 36
 Terebrantia, 107
 tergites, 43
 termitarium, 214
 termites, 212
 fossil, 274
 in France, 215
Termitodiscus, 225
 termitophiles, 224
Termitoxenia, 225
 testes, 73
 Tethys, 233
Tetracha carolina, 294
 Tettigoniidae, fossil, 285
 Tettigonioidae, 284
Thanasimosphaeria haasei, 310
Thaumatoxena, 225
 thermotropism, 138
 thigmotropism, 146
Thinnfeldia odontopteroides, 318
 thorax, 42

Thysanoptera, 108
 fossil, 205
 Thysanopteroidea, 239
 Thysanura, 90, 241
 tibia, 46
Tillyardagrion, 264
Tillyardiella, 255
 time-scale, geological, 231
Titanus giganteus, 27
 tools, use of by insects, 189
 touch, organs of, 67
 sense of, 136
 tracheae, 61
 operation of, 125
 tracheal gills, 59, 127
 traps, 164
Triacma, 294
 triangulin larva, 82
Triassagrion, 264
 Triassocorisidae, 310
 Triassolestidae, 261
Triassopsychops, 296
 trichomes, 212
 Trichoptera, 103
 fossil, 299
 mouthparts of, 39
 Trichopterygidae, 27
 Trilobita, 22
Triplectides, 299, 318
Triplosoba, 314
 Triplosobidae, 256
 trochanter, 45
 tropisms, 137
Tsekardocoleus, 290, 316
 tympanal organs, 70
Typus, 258, 315
 Tyrrhenian fauna, 321

U

'Ur-Insekten', 243
 urogomphae, 55
 uropod, 56

V

vacuoles, 64
 vannal field of wing, 49
 veins of wing, 50
 vertex of head, 31
 visceral nerve-system, 66
 vitellus, 74
 viviparity, 83

W

walking in insects, 157
 warning colours, 177

wasps, social life of, 200
wax production, 124
 secretion, 124
winged insects, origin of, 311
wings, 49
 evolution of, 85
wing venation, 51

X

xylophagous insects, 116

Y

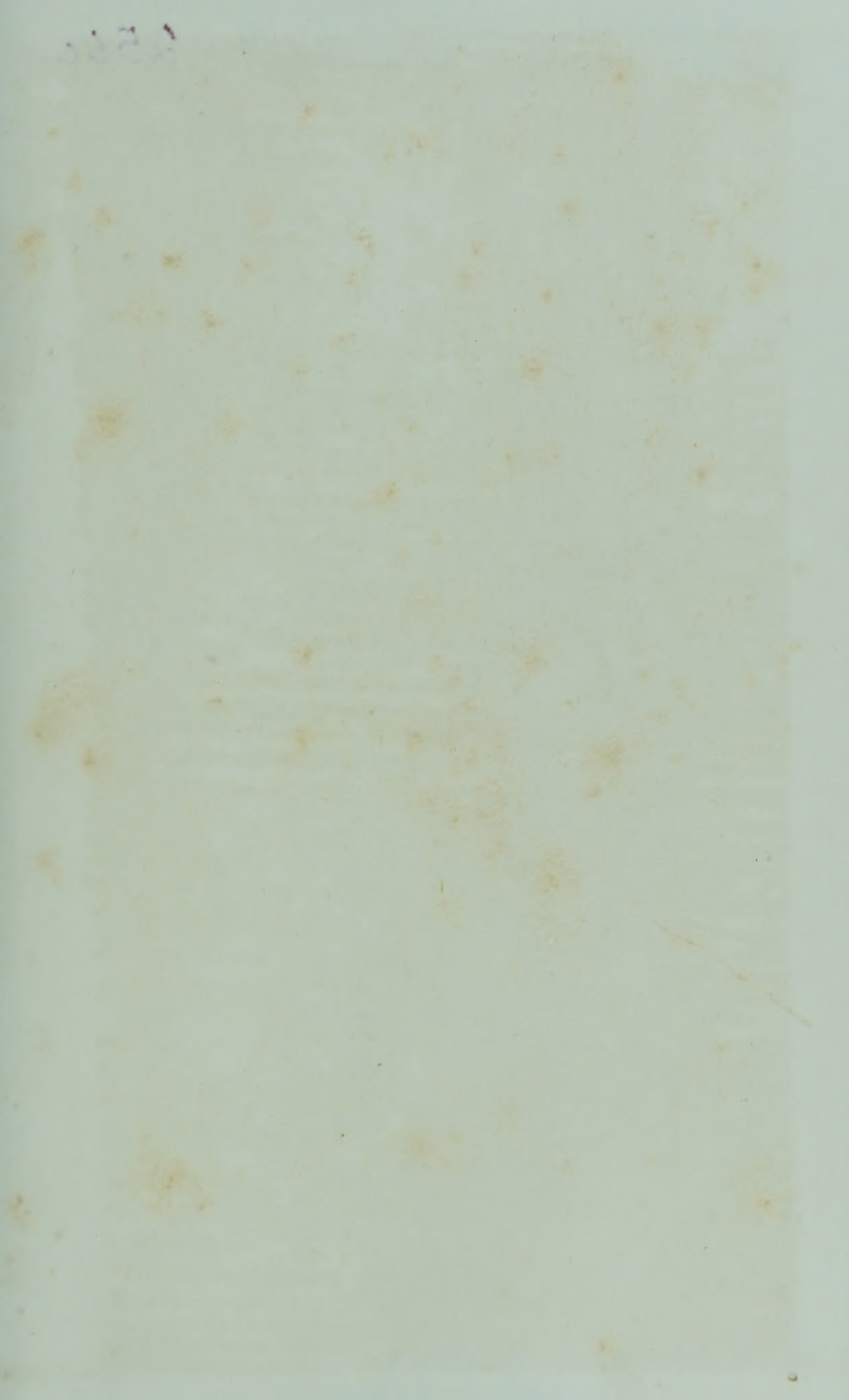
young, care of, 151

Z

Zoraptera, 99, 274

Zorotypus, 99

Zygoptera, 98



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